BOTANY

UNIVERSITY OF NEBRASKA LIBRARY NOV 29 1926

Volume LXXXII Number 3

The BOTANICAL GAZETTE

FOUNDED BY JOHN M. COULTER

NOVEMBER 1926

Vascular Tissues of Microcycas calocoma — Mintin A. Chrysler — 233

An Ecological Study in Utah. Contributions from the Hull Botanical Laboratory 356 — P. Alice Evans — 253

Seasonal Development of Growth Layers in Fraxinus campestris and Acer saccharinum — Herbert C. Hanson and Bernice Brenke — 286

Effect of Light Intensity on Growth of Soy Beans and Its Relation to the Autocatalyst Theory of Growth. Contributions from the Hull Botanical Laboratory 357 — Henry W. Popp — 306

Effect of Certain Deficiencies on Nitrogen Metabolism of Plants — R. C. Burrell — 320

Carpeloid Stamens of Podophyllum peltatum — M. Louise Sawyer — 329

Cosmos Blakei, a New Species from Guatemala. Contributions from the Hull Botanical Laboratory 358 — Earl Edward Sherff — 333

Briefer Articles

Structural Weaknesses in Interspecific Grafts of Pyrus — E. L. Proebsting — 336

Current Literature

Book Reviews — 339

Notes for Students — 342

THE UNIVERSITY OF CHICAGO PRESS
CHICAGO, ILLINOIS, U.S.A.

THE CAMBRIDGE UNIVERSITY PRESS, London
THE MARUZEN-KABUSHIKI-KAISHA, Tokyo, Osaka, Kyoto, Fukuoka, Sendai
THE COMMERCIAL PRESS, LIMITED, Shanghai

Volume LXXXII Number 3

THE BOTANICAL GAZETTE

A JOURNAL EMBRACING ALL DEPARTMENTS OF BOTANICAL SCIENCE

Editors

HENRY C. COWLES
JOHN M. COULTER, Emeritus

Associate Editors

CHARLES JOSEPH CHAMBERLAIN, Morphology
MERLE CROWE COULTER, Genetics
SCOTT VERNE EATON, Physiology
GEORGE DAMON FULLER, Ecology
WILLIAM JESSE GOAD LAND, Morphology
GEORGE KONRAD KARL LINK, Pathology
ADOLPH CARL NOÉ, Paleobotany
CHARLES ALBERT SHULL, Physiology

Issued November 24, 1926

The Botanical Gazette is published in eight issues annually (omitting January and February, and July and August) by the University of Chicago at the University Press, 5750 Ellis Avenue, Chicago, Ill. ¶The subscription price is $9.00 per year; the price of single copies is $1.25. Orders for service of less than a half-year will be charged at the single-copy rate. ¶Postage is prepaid by the publishers on all orders from the United States, Mexico, Cuba, Porto Rico, Panama Canal Zone, Republic of Panama, Dominican Republic, El Salvador, Argentina, Bolivia, Brazil, Colombia, Costa Rica, Ecuador, Guatemala, Honduras, Nicaragua, Peru, Uruguay, Paraguay, Hawaiian Islands, Philippine Islands, Guam, Samoan Islands, and Spain. ¶Postage is charged extra as follows: For Canada and Newfoundland, 30 cents on annual subscriptions (total $9.30); on single copies 4 cents (total $1.29); for all other countries in the Postal Union, 60 cents on annual subscriptions (total $9.60), on single copies 8 cents (total $1.33). ¶Patrons are requested to make all remittances payable to The University of Chicago Press in postal or express money orders or bank drafts.

The following are authorized to quote the prices indicated:

For the British Empire: The Cambridge University Press, Fetter Lane, London, E.C. 4, England. Yearly subscriptions, including postage, £2 8*s*. each; single copies, including postage, 6*s*. 8*d*. each.

For China: The Commercial Press, Limited, Paoshon Road, Shanghai. Yearly subscriptions, including postage, $9.60; single copies, including postage, $1.33, or their equivalents in Chinese money.

Claims for missing numbers should be made within the month following the regular month of publication. The publishers expect to supply missing numbers free only when losses have been sustained in transit and when the reserve stock will permit.

Business correspondence should be addressed to The University of Chicago Press, Chicago, Ill.

Communications for the editor and manuscripts should be addressed to the Editor of the BOTANICAL GAZETTE, The University of Chicago, Chicago, Ill.

Contributors are requested to write scientific and proper names with particular care, to use the metric system of weights and measures, and in citations to follow the form shown in the pages of the BOTANICAL GAZETTE.

Papers in excess of thirty-two printed pages are not accepted unless the author is willing to pay the cost of the additional pages, in which case the number of the pages in the volume is correspondingly increased. Carbon copies of manuscripts will not be accepted.

Illustrations are furnished without cost to author only when suitable originals are supplied. Plates in excess of four are not accepted unless the author is willing to bear the additional cost. A copy of the suggestions made in the April number, 1916, will be sent on application. It is advisable to confer with the editors as to illustrations required in any article to be offered.

Separates, if desired, must be ordered in advance of publication. A table showing approximate costs of separates is printed on an order blank which accompanies the proof; a copy will be sent on request.

Entered as second-class matter August 21, 1896, at the Post-Office at Chicago, Illinois, under the Act of March 3, 1879.

Acceptance for mailing at special rate of postage provided for in Section 1103, Act of October 3, 1917, authorized on July 15, 1918.

PRINTED IN THE U.S.A.

T

N

T

Th
a
un
ie
of
th
k
th
m
g
m
m
a
g
o
fr
to
s
th
y
to
m
P
d
P
T
t
s
t
T
P
V
V
T
t
T
P
P
C

The PRESS IMPRINT

November and December 1926

The World and Man

The advance of modern science has revealed a vast store of fascinating facts about the universe in which we live. More discoveries have been made in nearly every branch of science in the past two or three decades than in all the previous history of mankind. Scientists have disclosed a world of the infinitely small in electrons, atoms, and molecules; and of the enormously large in giant suns and galaxies of stars, billions of miles distant. They have looked back millions of years to the origins of worlds, and have traced their history through the geological ages to the present. Myriads of plants and animals have been studied, from the lowliest bacteria and protozoa up to man. Minute investigation of man himself—his origin, the wonders of his body, the development of his intelligence—has yielded astonishing facts. Inanimate matter has revealed marvelous secrets to the modern chemist. The physicist has explained the forces we see about us every day, and the biologist is seeking to explain the very secret of life itself.

To help the inquiring reader in his efforts to keep up with the procession of modern science, sixteen members of the Faculty of the University of Chicago have written *The Nature of the World and of Man*, which E. E. Slosson describes as a book for "those who have not been to college and those who have."

These men, specialists in their fields, are the authors: Forest Ray Moulton, Rollin T. Chamberlin, J Harlen Bretz, Harvey B. Lemon, Julius Stieglitz, Horatio Hackett Newman (the editor), Edwin Oakes Jordan, Merle C. Coulter, Henry Chandler Cowles, Warder C. Allee, Alfred S. Romer, Fay-Cooper Cole, Elliot R. Downing, George W. Bartelmez, Anton J. Carlson, and Charles Hubbard Judd.

Beginning with the outstanding facts about the solar system, each of the sixteen authors has described that phase of development with which he is most familiar: the origin and early stages of the earth; geological processes and the earth's history; the nature of energy and matter; bacteria and their origin; evolution of the plant kingdom, the vertebrates, and the invertebrates; interactions between plants and their environment; the coming of man; organic evolution and the origin of life; human inheritance; structure of man; the living process; and mind in evolution.

Throughout, the authors have emphasized the conception of science as a glowing, living thing inextricably bound up with every human life. With all its multiplicity of authorship, the book has (in the words of the *Chicago Tribune*) "taken on the unity, the coherence, the march of one great epic poem."

Stuart Pratt Sherman said not long ago: "I have a strong impression that our 'average' American is waking up, responding to the new emphasis on 'adult education,' becoming infatuated with the idea of having his education go on as long as he does. He has got wind of the secret that in all the fields of knowledge enormous changes and advances have been made in the last twenty-five years and are still being made at this present hour. His sporting desire to keep up with his times grows keener and the range of his curiosity will soon be encyclopedic."

The popularity of *The Nature of the World and of Man* is evidence of the awakening of the adult public to the possibilities of

further education. For the reader outside the universities the book is a guide to the world of contemporary science; it enables him to form a conception of how the earth came to be, what its place is in the vast physical universe, how life originated; it gives him glimpses of the monsters of early ages; shows him how Cro-Magnon man lived, how atoms are held together in a molecule, how invisible throngs of bacteria surround us, how life came from the sea to the land, why insanity is increasing, how speech developed, how hormones regulate bodily processes. . . . .

The Nature of the World and of Man contains the subject matter of a "survey course" given each year by its authors to a selected group of beginning students at the University of Chicago. The success of the experiment upon which it is based suggests a wide use of this text in similar courses in other institutions to give the beginner a preliminary view of the surrounding world and of his possible function in it.

In this day of increasing specialization and a confusingly large body of human knowledge, orientation toward the more general aspects of the world and of man is a necessity. In the belief of the authors of this text, orientation may best begin with a presentation of what modern science holds as truth. They have therefore attempted to give the student that acquaintance with the general outlines of scientific thought which is the ideal point of departure for his entire intellectual development, and which alone affords him the proper perspective on the world of modern thought. More specialized courses in thinking, man in society, or the arts, may well follow, but this course, being more informational, more inclusive, and easier for the beginner should be the point of departure. *THE NATURE OF THE WORLD AND OF MAN.* By SIXTEEN MEMBERS OF THE FACULTY OF THE UNIVERSITY OF CHICAGO. *$4.00, postpaid $4.15.*

* * *

Current American Prose

In a volume of provocative essays, *The Outlook for American Prose*, Joseph Warren Beach searches the current prose of reflection, reminiscence, criticism, and social commentary for auguries of a first-rate style. He judges as stylists the American prose artists who are now in the public eye. Timely and incisive comment from this candid and erudite observer will be not unwelcome to readers who have become aware of the development of American prose style in such books as *Troubadour*, *Straws and Prayer-Books*, and *A Story-Teller's Story*.

A professed eclectic, and adherent of no particular school or tendency, Mr. Beach seeks the perfect style wherever it may be found. Looking about for American writers of cultivated philosophical prose to compare with Bertrand Russell and Havelock Ellis; biographers to rank with Lytton Strachey; newspaper essayists to place beside Chesterton; and critics as stimulating as Shaw, he advances a gratifying number of claimants to distinction. In Sherwood Anderson, James Branch Cabell, H. L. Mencken, Stuart Pratt Sherman, Paul Rosenfeld, Simeon Strunsky, and Alfred Kreymborg, Mr. Beach finds the most hopeful signs of a distinguished prose art in America, and whether or not you agree with him, you will have to reckon with his arresting dicta on the luminaries of the day.

"Old fashioned or new fashioned, what we want is something first rate," says Mr. Beach. His regard for stylistic perfection leads him to protest against the incoherence of Hergesheimer; the lack of precision in John Dewey; the naïveté of Dreiser; the scientific jargon of Van Wyck Brooks; and the affectations of Van Vechten. Sentimental violence and overuse of such words as "devastating" and "poignant" are charged against Ben Hecht, Hutchinson, Walpole, and Hergesheimer.

SHERWOOD ANDERSON

—"*A prose-writer who dares to use the devices of the poet.*"

Mr. Beach finds Gamaliel Bradford too serious minded and turns for lightness of touch to Strunsky and Morley. In Anderson, Cabell, Mencken, and Sherman, he finds the supreme qualities of flavor and individuality, gusto, and precision. Kreymborg's style is "uniformly graceful, delicately tinted."

VAN VECHTEN

—"*Baedeker of the intelligentsia.*"

Mr. Beach has put to good use a conception of the genuine critical spirit characterized by candor and tolerance. He admits that he has been denied that arrogance which enables a critic to tell at a glance whether or not a writer is one of the immortals. First-rate prose he finds most frequently in the unpretentious styles that slip in between rigid categories.

You will want to read this book for the vigor of its outlook upon American prose and for its timely comment on some of the most interesting figures in modern literature.

H. L. Mencken says in the *American Mercury:* "This is perhaps the first book, written by an American, in which precept is backed up by practice. Mr. Beach writes very effectively, and has much of interest to say. His judgments on the writing of Dreiser, Anderson, Van Vechten and other living Americans are well-informed and plausible." *THE OUTLOOK FOR AMERICAN PROSE.* By JOSEPH WARREN BEACH. *$2.50, postpaid $2.60.*

* * *

New Version of the Psalms

For a long time we have needed a translation of the Book of Psalms into the language of our day—a translation that would give the modern reader new insight into the classical rendering of the King James Version, and enable him to see in the Psalms the meaning they originally had. Such a translation is the new version by J. M. Powis Smith, which removes the stumbling-blocks of a centuries-old vocabulary, and divests the verses of unwarranted meanings which a succession of early translators read into them. This version is based upon the official Hebrew text, corrected and emended in accordance with the findings of present-day scholarship.

Dr. Smith expresses at the outset his admiration for the King James Version of the Psalms as "a masterpiece of English literature, unrivalled in beauty," and disclaims any attempt to supplant it with his own version. His purpose is rather to express, as completely and as accurately as the limitations of language permit, the thought and feeling of the original; and to incorporate the scholarship of recent decades, with its more thoroughgoing text-critical method and improved philological results. His aim has been at all times to create a clear and uncorrupted version in which the reader of today will be able to see unhampered the beauties and true meaning of the world's greatest hymnbook.

This translation is intended for the public rather than for technical study; it is not, however, an attempt to bring the Psalms down to the level of the mythical "man on the street." The Psalms are here reproduced in a language and style befitting their spirit and content.

While seeking to avoid a bald literalism, Dr. Smith has preferred to err on that side rather than upon the side of paraphrastic expansion. His aim being always accuracy of meaning, he has chosen not to take the liberties of paraphrastic rendering.

The translator brings to his task unusual qualifications. He is professor of Semitic languages and literatures in the University of Chicago, editor of the *American Journal of Semitic Languages and Literatures*, and one of the foremost Hebrew scholars in this country. He is the author of several well-known books on Old Testament subjects.

This version of the Psalms is the first step in the complete American translation of the Old Testament, upon which a committee of Hebrew scholars is now working and which will require a year for its completion.

In this rendering, the modern reader can now read the Psalms in the language of his own day, just as they were written centu-

Methods in Plant Histology

Fourth Edition

By

CHARLES JOSEPH CHAMBERLAIN

So extensive have been Professor Chamberlain's revisions that he has given us practically a new book. Rewritten throughout, it brings up to date the methods for preparing all kinds of plant structure for microscopic study.

Killing and fixing, sectioning, staining, the paraffin, Venetian turpentine, celloidin, and glycerine methods are treated, and chapters on making photomicrographs and lantern slides have been added. Even in the universally used paraffin method there has been improvement in fixing, infiltration, and imbedding, and American stains have been successfully used. The Venetian turpentine method has been brought to a high degree of efficiency, and now occasions little difficulty even for a beginner. The cellulose acetate method, which is entirely new, has also been introduced.

Methods in Plant Histology may be used in classes under an instructor but the directions are explicit, and now, more than ever, it will help the student working alone learn to make first-class preparations.

$3.25, postpaid $3.37

THE UNIVERSITY OF CHICAGO PRESS

CHICAGO · ILLINOIS

ries ago. Now as never before he can see clearly reflected the religious and spiritual conceptions of the greatest of hymnbooks. *THE PSALMS*. Translated from the Hebrew by J. M. POWIS SMITH. *$3.00, postpaid $3.15.*

* *

Introducing Urban Sociology

A new volume, *The Urban Community*, edited by E. W. Burgess, and a previously published one, *The City*, by Robert E. Park, E. W. Burgess, and others, form together a much-needed introduction to an urban sociology. They are the nearest approach thus far to textbooks in urban sociology, including under that term community organization, urban geography, and human ecology. Based upon a conception of the city as a living organism, they are the first steps in an attempt to supply that basic understanding of the city needed to unify the many present-day urban movements. These two books offer an introduction, not merely to the facts of urban life, but to the processes involved in human life from the standpoint of environment.

Continuing the work of outlining the field of urban sociology as begun in *The City*, the new volume, *The Urban Community*, is a prospectus of the present state and promise of sociological research in this field. It indicates and illustrates for students of the subject the different techniques of research, ecological, cultural, and statistical, which are being applied to the study of the city.

It covers a wide range of phenomena from human nature and personality to statistics of city life. It deals with fundamental problems and contains more modern applications of the subject and more statistics on urban problems than any other volume. It will be a most helpful text for teachers of urban sociology and community organization, and will admirably aid all students of these subjects, as well as those interested in urban geography.

The chapters in this volume are selections from the proceedings of the 1925 meeting of the American Sociological Society.

*

In *The City* a group of sociologists brought to the study of urban problems a technique

which assured a more searching and disinterested analysis than had previously been attained. This pioneer work is concerned with outlining a program for future investigation of human nature and social life under modern urban conditions.

A wide variety of phenomena characteristic of city life have been investigated: from the metropolitan daily newspaper to "Magic, Mentality, and City Life." This book directs the student toward investigation of the physical organization, the occupations, and the cultures of the city, and gives him a conception of the ecological approach to the city. *THE URBAN COMMUNITY*. Edited by E. W. BURGESS. *THE CITY:* Human Behavior in the Urban Environment. By ROBERT E. PARK, E. W. BURGESS, AND OTHERS. *Each $2.00, postpaid $2.10.*

* * *

The Inside Story of Chicago Politics

A realistic story of Chicago politics as evidenced in the primary of 1926 has been told by a disinterested observer, a political scientist concerned with bringing to light actual election methods; and is offered to the public in *The Chicago Primary of 1926* by Carroll H. Wooddy. This book is based upon extensive first-hand investigation; it goes back of the shifting tides of political warfare to an understanding of what makes Chicago politics what it is. This volume is not campaign literature; it is absolutely nonpartisan, studying all factions alike, and is motivated entirely by the need for a scientific understanding of political phenomena.

The public sees only the final alignment of forces, the line-up of political allies and combatants, the long slates of rival candidates. What went on before, how a particular combination came to be made, is only vaguely understood. There is a saying that politics makes strange bedfellows, but there are causes of political expediency behind these often peculiar combinations. These causes have been clearly shown by Mr. Wooddy. He traces the development of each faction from the time of Busse, Lorimer, Deneen, and Dunne to the present day, records the quarrels and compromises needed to bring about definite alignment,

Teaching Science in the Schools

By

ELLIOT R. DOWNING

Scientific study of science teaching has had some valuable results, and these Mr. Downing summarizes in this volume. Here is shown how the growing body of facts about the pedagogy of science, which have been ascertained by the experimental method, may be applied practically to the problems of the science teacher.

This book describes the social and economic background of the science-teaching movement, the history of science teaching in our elementary and secondary schools, present conditions in science teaching, and the aims held.

From this point Mr. Downing takes up the principles of selection and organization of science materials, and actual methods of instruction—by book, lecture-demonstration, and laboratory. There is specific information on notebooks and drawings, field trips, testing results; and suggestions are made for a complete science library in the school.

$2.00, postpaid $2.10

THE UNIVERSITY OF CHICAGO PRESS

CHICAGO · · ILLINOIS

REVISED EDITION

Evolution, Genetics, and Eugenics

By

HORATIO HACKETT NEWMAN

Attendance at the Dayton trial as a witness for the defense has enabled Professor Newman to describe and interpret it in this new revised edition of his text. He brings the knowledge of the evolutionary biologist to bear upon the present anti-evolution campaign in the United States, and studies it historically, giving the facts about evolution needed for an intelligent attitude toward the controversies.

The discussion of mutation, linkage and crossing-over, inheritance of acquired characteristics, eugenics, and other topics has been brought completely up to date. Here in a single volume is a comprehensive treatment of all the important phases of evolutionary biology that takes account of recent developments.

Original material by Professor Newman weaves together a well-balanced selection of excerpts from such writers as Darwin, Weismann, Romanes, and Castle. This is an excellent text for survey courses in evolutionary biology and a clear treatment for the general reader.

$3.50, postpaid $3.70

THE UNIVERSITY OF CHICAGO PRESS

CHICAGO · · · ILLINOIS

shows how the slates of candidates are made up in the conclaves of the leaders, and judges the extent to which the direct primary has eliminated the bad features of previous methods.

The extent to which the old slogan "to the victors belong the spoils" still operates in Chicago politics has seldom been analyzed as thoroughly as in this book. Mr. Wooddy indicates the copious political spoils contested for by the various factions, sources, in the main of personal and political power, which can be used to build up a powerful machine. He finds prevalent the type of politics whose medium of exchange is votes, and whose compensations are jobs.

The voter is asked to support candidates upon certain issues, but often he has no way of knowing to what extent the issues are handpicked as political ammunition or to what extent they represent the convictions of the candidates. Mr. Wooddy analyzes the processes by which campaign issues are selected and supported, what appeals are made, and shows how issues irrelevant to the situation are often dragged in because they offer an opportunity for good political showmanship.

The voter is often in doubt as to whether civic agencies—better government associations, voters' leagues, newspapers, etc.—are "on the level." Are civic agencies ever corrupted by machine politics? Do newspapers distort the news in the interests of various factions? Mr. Wooddy's investigation and analysis of these questions gives the public a basis for a reasoned judgment.

This book is one of a few genuinely realistic pictures of concrete political situations, and is, at the same time, entirely impersonal and dominated by no political motives. It opens windows through which the voter is seldom permitted to gaze, revealing the inner workings of a great political and factional organization. Journalistic in style, it preserves the flavor of the actual situation. Here is a fascinating story of the jungle of factions and feuds in Chicago political life, an account which unravels the puzzling web of the personal connections of the politicians and the complicated social groups behind them. *THE CHICAGO PRIMARY OF 1926.* A Study of Election Methods. By CARROLL H. WOODDY. *$1.50, postpaid $1.60.*

The Origin of the Earth

By

THOMAS C. CHAMBERLIN

The story of a research, the steps and methods of an inquiry, and the exposition of a new theory of the formation of the earth are woven together in this volume. The inquiry started two decades ago in the study of the glacial problem; it led through the enigmas of earlier climatic states, and created grave doubts as to the truth of the conception of a once molten globe enveloped in great, hot atmospheres.

Mr. Chamberlin discusses the disclosures that led to the rejection, one after another, of older views of the origin of the earth, including the nebular hypothesis of Laplace. He describes the futile attempts to emend these theories or to build others on the same foundations, and, finally, traces the steps in the construction of his own, radically new view, based on a dynamic foundation.

$2.00, postpaid $2.10

THE UNIVERSITY OF CHICAGO PRESS

CHICAGO · · ILLINOIS

A Check-List for This Month

The University of Chicago Press
5750 Ellis Avenue, Chicago, Illinois

GENTLEMEN:

Please send me the following books ☐ for examination ☐ for which I inclose $_____.

☐ *The Nature of the World and of Man.* By SIXTEEN MEMBERS OF THE FACULTY OF THE UNIVERSITY OF CHICAGO. (*$4.15, postpaid.*)

☐ *The Outlook for American Prose.* By JOSEPH WARREN BEACH. (*$2.60, postpaid.*)

☐ *The Psalms.* Translated from the Hebrew by J. M. POWIS SMITH. (*$3.15, postpaid.*)

☐ *The Urban Community.* Edited by E. W. BURGESS. (*$2.10, postpaid.*)

☐ *The City.* By ROBERT E. PARK, E. W. BURGESS, AND OTHERS. (*$2.10, postpaid.*)

☐ *The Chicago Primary of 1926.* By CARROLL H. WOODDY. (*$1.60, postpaid.*)

☐ _____

☐ _____

☐ _____

☐ _____

☐ _____

☐ _____

Name_____

Address_____

LEMON

MOULTON

BRETZ

CARLSON

JORDAN

THE NATURE OF THE WORLD AND OF MAN

By

SIXTEEN MEMBERS OF THE FACULTY OF THE UNIVERSITY OF CHICAGO

BARTELMEZ

COWLES

So extensive a program as this book presents has seldom been attempted, much less accomplished so successfully. It is an outline of our knowledge of the physical and biological world and man's relative position in it: a bird's-eye view of the universe in the light of modern science.

This volume contains the subject-matter of a "survey course" given each year by its authors to a selected group of beginning students at the University of Chicago. The success of the experiment upon which it is based suggests a wide use of this text in similar courses in other institutions to give the beginner a preliminary view of the surrounding world and of his possible function in it.

NEWMAN

COLE

Beginning with the outstanding facts about the solar system, each of the sixteen authors has described that phase of development with which he is most familiar: the origin and early stages of the earth; geological processes and the earth's history; the nature of energy and matter; bacteria and their origin; evolution of the plant kingdom, the vertebrates, and the invertebrates; interactions between plants and their environment; the coming of man; organic evolution and the origin of life; human inheritance; structure of man; the living process; and mind in evolution.

CHAMBERLIN

$4.00, postpaid $4.15

COULTER

THE UNIVERSITY OF CHICAGO PRESS

CHICAGO · ILLINOIS

ROMER

DOWNING

STIEGLITZ

JUDD

ALLEE

VOLUME LXXXII NUMBER 3

THE

BOTANICAL GAZETTE

November 1926

VASCULAR TISSUES OF MICROCYCAS CALOCOMA

MINTIN A. CHRYSLER

(WITH PLATES XVI–XVIII AND THREE FIGURES)

Microcycas is the most accessible of the treelike cycads to a student in this part of the world, yet its structure and life history are imperfectly known. The extremely narrow range of this monotypic genus, and the apparently small number of individuals render a careful study desirable. With the special object of securing properly preserved material of the phloem of an arboreous cycad, a journey to western Cuba was undertaken in the summer of 1924. In this connection it is a pleasure gratefully to acknowledge the favor of a grant from the research fund of the New York Academy of Sciences. Acknowledgment is also made to the following persons, who have supplied material or aided in its collection: Professor C. J. CHAMBERLAIN of the University of Chicago, Director N. L. BRITTON of the New York Botanical Garden, Dr. O. W. CALDWELL of the Lincoln School, New York City, Director G. W. FORTUN of the Estacion Agronomica of Cuba, Dr. J. T. ROIG, Botanist of the same station, Mr. H. A. VAN HERMANN, Santiago de las Vegas, Cuba.

Field observations

The plant was studied at two stations, San Diego de los Baños and Consolacion del Sur, both in the province of Pinar del Rio, western Cuba. In the neighborhood of San Diego the plant was found on the slopes of the siliceous rounded hills locally known as "lomas." The station near Consolacion, however, is in nearly level

country south of the Santa Catalina range, the plants occurring to the number of about a dozen along a small water course. CALDWELL'S (2) observations indicate that "the plants are closely limited in elevation, the level showing them to be at essentially the same elevation, although they vary greatly in their distances from the tops of the mountains upon which they grow." The healthy appearance of the specimens at Consolacion, and the presence of a cone on nearly every individual show that a high altitude is not necessary for the proper development of the plant. At the same time, no seeds or young seedlings were found, so it is improbable that the species is extending its range. Provided suitable conditions are present, the plant shows good capabilities for vegetative reproduction, for instance by sprouts. At San Diego a specimen was observed which had been bent over and had assumed an S shape, with an extra crown arising at the summit of the convex arm of the S.

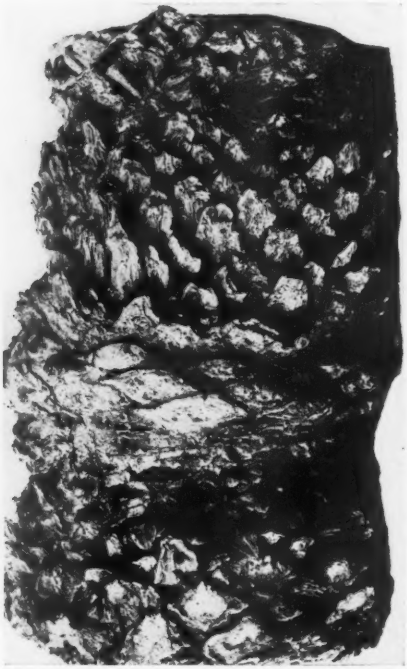


FIG. 1.—Portion of trunk, showing wide zones covered with scales and narrow zones occupied by leaf bases; ×0.5.

So far as can be ascertained, the total number of individuals within the very restricted range is decidedly small, and the plant is sought for several reasons.[1] The extremely slow growth of the plant,

[1] The local name "palma corcha" is applied because of the use of the seeds as bottle corks.

its occurrence in small detached groups, and the existence of solitary aged specimens, as recorded by CALDWELL, plainly indicate that this rare plant is rapidly nearing extinction. It was with much satisfaction, therefore, that the writer learned that the Cuban government has lately taken action in prohibiting the removal of specimens of the plant.

Trunk

The considerable height (up to 30 feet) of mature specimens has been recorded by CALDWELL (2) and CHAMBERLAIN (6). The measurements in the present paper are from a specimen about ten feet high, which was cut down at the station near Consolacion del Sur. Both of the writers just named figure the conspicuous rings or circular ridges which occur rather irregularly at intervals of a few inches. In the upper part of a trunk it is easy to see on the rings the scars left by the fallen leaves, which have been cut off by an absciss periderm, as described by CHAMBERLAIN for *Dioon* (5). The wide spaces bebetween the rings are occupied by the ragged bases of scale leaves. The general appearance is shown in fig. 1, taken from a piece of stem somewhat more than a foot below the apex. A comparison with CHAMBERLAIN'S figure of the trunk of *D. spinulosum* (5) shows that in the latter genus the relation between leaf bases and scale bases is reversed, namely, the zones of leaf bases are the broad ones, and the zones of scales are quite narrow. It is obvious that in *Microcycas* the number of ridges indicates the number of crowns which have been produced by the plant. If one could be certain as to the frequency with which the new crowns are produced, it would be easy to approximate the age of a specimen, for the ridges are quite persistent. A reliable observer at the Experiment Station at Santiago de las Vegas reports that the four plants which are growing at the Station produce a crown every two years. Dr. JUAN T. ROIG has very kindly undertaken to measure the intervals between the rings on the trunks of the four specimens just mentioned, and his measurements yield the following figures:

Plant no. 1, 19 rings in distance of 9 ft. 4 in.; average interval 6 in.
Plant no. 2, 37 rings in distance of 9 ft.; average interval 3 in.
Plant no. 3, 18 rings in distance of 6 ft.; average interval 4 in.
Plant no. 4 (less than 5 ft. high).

These figures give a value of almost exactly 4 inches as the average distance between rings in specimens growing under rather favorable conditions. If a new crown is produced every two years, a plant obviously increases its height by 2 inches per year, or a tree 10 feet high would be somewhat over 60 years old, since the growth in height is less rapid during the first few years of the plant's life. Such an estimate corresponds fairly with CHAMBERLAIN'S figure for *Dioon spinulosum*, where a tree 20 feet high is calculated to be over 100 years old, on the assumption that a crown is produced every year.

FIG. 2.—Part of transverse cut through trunk, showing wide pith and cortex and narrow vascular ring with rays; cortex shows a few of the girdling leaf traces; ×0.66.

A section taken transversely through the trunk shows the usual cycadean condition of an exceedingly wide pith, a narrow vascular ring, and a broad cortex surrounded by the bases of leaves or scales (fig. 2). It will be observed that the trunk of *Microcycas* is monoxylic, in contrast with such genera as *Cycas* and *Macrozamia*. Longitudinal cuts through the trunk display also at intervals the "cone domes" or vascular supply of cones, corresponding to CHAMBERLAIN'S fig. 4. It has not been possible in *Microcycas* to match these cone domes with the external rings. The following measurements are contributed for comparison with those furnished by CHAMBERLAIN (**5**): in a trunk of *Microcycas* about 3 m. high, at a distance of 300 mm. from the apex the diameter of the trunk was 110 mm., pith 65 mm., thickness of xylem 4 mm., of phloem 2 mm., and of cortex

16 mm.; while at a distance of 2500 mm. from the apex the diameter of the trunk was 120 mm., pith 72 mm., thickness of xylem 9 mm., of phloem 5 mm., and of cortex 10 mm. These figures correspond very nearly with those for all but the very old stem of *Dioon*.

Histology of stem

TECHNIQUE.—Material was fixed soon after collection in JEFFREY'S corrosive sublimate-picric acid mixture, which was found to be entirely suitable. In the early part of the study the abundant starch contained in the stems was partly removed by digesting at 50° in diastase solution, but it was later found that the material imbedded readily in celloidin without preliminary digestion, after treatment with hydrofluoric acid. With material thoroughly infiltrated, no difficulty was experienced in cutting sections sufficiently thin for photographing. The sections were stained in Haidenhain's haematoxylin, followed by safranin, mounted in balsam, and finally flattened by spring clothes pins.

XYLEM.—In general the xylem of *Microcycas* corresponds in structure to that of the other monoxylic genera, namely, it consists of tracheids, wood parenchyma, and rays, certain of the last carrying leaf traces. The general relations of these as seen in transverse section are shown in fig. 4. The parenchyma cells may clearly be distinguished from the tracheids by the single contour of the former. The essential similarity of this wood to that of *Dioon* may be seen by comparison with CHAMBERLAIN'S fig. 20, in which case, however, no parenchyma cells are shown, although they occur plentifully in that genus, as shown by independent observation, and indicated by CHAMBERLAIN'S fig. 17. The woody elements are grouped in narrow radial strips from one to about four cells in width, separated by the rays. The tangential diameter of the mature tracheids is about 45 μ, and the length varies widely, ranging from 3.7 to 8 mm., with average at 6 mm. These measurements correspond closely to those taken by Miss LANGDON in her study of the stem of *Dioon* (**9**), and show that the tracheids of cycads are definitely longer than are those of conifers, for the average length of the tracheids of 29 species of conifers listed by RECORD (**14**) is 3.77 mm.

The nature of the protoxylem in cycads has been called in ques-

tion, and even its occurrence in the adult stem has been doubted. One reason for difficulty in finding protoxylem in an old stem, as METTENIUS (11) pointed out and figured long ago, is the eventual fragmentation of the inner layers of xylem owing to the growth and division of parenchymatous cells in the outer region of the pith (fig. 15), leading not only to separation of the elements, but also to throwing many of them out of perpendicular. MILLER (12) correctly states that the early tracheids pursue an undulating course, which makes them hard to follow (this however does not apply to a tangential section). In material taken from within a foot of the stem apex in *Microcycas*, however, it is easy to be certain that one is dealing with actual protoxylem. The tracheids at the tip of one of the xylem wedges shown in figs. 14 and 23 fulfil at least two of the requisites for being regarded as protoxylem. (1) They are narrow, their diameter being about 10 μ, while that of the tracheids of the mature secondary wood ranges around 45 μ. (2) They are not heavily lignified, as shown by the phloroglucin test, but they rarely show a steep or broken spiral thickening, and are rather characterized by a close spiral thickening which quickly merges in later-formed tracheids into a reticulate or scalariform thickening located on all faces of a tracheid, but devoid of border. The absence of conventional protoxylem with steep spirals might be accounted for by the supposed collapse or destruction of such elements during growth of the stem. METTENIUS endorses such an explanation in the case of *Cycas revoluta*, and describes ring and spiral tracheids in the inner part of the stele of a sufficiently young plant. MILLER, however, finds in *C. media* that "protoxylem elements are usually scalariform, although hints of spiral tracheids are more or less frequent." He observes, moreover, "since neither transverse nor radial preparations show crushed masses of cellular material at the centripetal ends of the bundles, there can be no doubt that the xylem elements which can be seen to terminate the bundles are truly protoxylem, whether they are spiral or scalariform." In other words, it is the nature of a cycad to produce protoxylem of the scalariform rather than spiral type in its stem. It will be seen later that the petiolar bundles of *Microcycas* and other genera show a protoxylem with definite spirals which are more or less disorganized, as though pulled out. It might

be argued that the cycad leaf undergoes great extension, while the stem lengthens very slowly, but the absence of steep spirals in the rapidly elongating leader of pine or fir casts much doubt on this explanation. The stresses present in the stem tip of cycads appear to be due to pressure rather than tension, owing to the great growth of the pith, leading to the pushing asunder of the primary tracheids, as was pointed out by METTENIUS, and as may be discovered in material of *Microcycas* cut several feet below the stem tip (fig. 15). On the whole it appears safe to conclude that the protoxylem of the cycad stem is of a somewhat advanced or abbreviated type, in which the spiral elements are few and the scalariform condition is quickly reached.

Contrasting with the precocity just credited to the protoxylem is the extreme slowness with which the secondary tracheids attain their typical or adult form. Although the bulk of the xylem in an old stem of *Microcycas* consists of pitted tracheids (fig. 6), the metaxylem and a considerable width of secondary xylem show only scalariform thickenings; at first fibrous, but farther out provided with a border to each mesh of the ladder, and followed by the well known transitional elements (fig. 7), which soon merge into tracheids whose radial walls are more or less thickly covered with bordered pits. The scalariform zone extends in some cases as many as 40 rows of tracheids, and this region may be regarded as the juvenile stage of the xylem. In this connection it is interesting to note that genera such as *Stangeria* and *Zamia*, which have a tuberous habit, appear never to get beyond this juvenile stage, for their secondary xylem consists entirely of scalariform tracheids, mixed of course with parenchyma. As may be seen in figs. 16 and 17, the scalariform tracheids of *Microcycas* show the bars on all sides, while the pitted tracheids have the pits restricted almost entirely to the radial faces, as is the case in *Dioon* and *Cycas* (**5, 12**).

The long gradual sequence of narrow spiral, narrow scalariform, wide scalariform, scalariform with border, transitional and finally pitted tracheids, furnishes a remarkable illustration of the recapitulation doctrine, and points to the low position of the cycads among the seed plants. The series is almost as complete, although not quite so gradual, as the classic case of *Cordaites* (*Dadoxylen*)

Brandlingii figured by SCOTT (**16**), PENHALLOW (**13**), and recently reexamined and discussed by BAILEY (**1**).

The growth rings which CHAMBERLAIN found so plain in the stem of *Dioon spinulosum* and *D. edule* could not be seen in the trunk of *Microcycas*. Pieces of stem which had lain for a time in iodine solution showed considerable difference in depth of staining in different layers of the xylem, but this was found to be due only to a large proportion of starch-bearing parenchyma in the deeply staining layers, and the layers were irregular and few in number. Radial sections of the wood, however, showed what may possibly correspond to growth rings, for the broad zone of scalariform tracheids previously described is more or less clearly segregated into about three layers, each made up as follows: eight or ten scalariform tracheids, then a transitional element followed by a rather plainly pitted element. After about three zones made up in this way, all of the tracheids are of the pitted or transitional type. About two zones of this sort were discernible in the material of *Dioon* kindly furnished by CHAMBERLAIN. These appearances are not sufficiently clear cut to be entirely satisfactory evidence of growth rings, but the observations seemed worthy of record.

The wood parenchyma does not appear to have any definite arrangement; isolated cells, radial groups of two or three, and tangential groups are all to be found. Like all other available storage space, these cells are filled in the living plant with the large starch grains which are characteristic of cycads. Crystals are not a conspicuous feature in the genus under consideration. The walls show numerous simple pits (fig. 6).

Rays of three sorts may be distinguished: uniseriate, multiseriate, and fusiform. The general disposition of these is shown in fig. 3. Rays 2–4 cells thick with a height of 15–30 cells are very common. The fusiform rays may have a thickness of 15 or more cells at the middle, and contain a leaf trace. The trace in the middle of fig. 3 shows a connection with the secondary wood (CHAMBERLAIN **5**, LANGDON **9**). Such connections are frequent, and play an important part in the functioning of the leaf traces after the leaf with which they were originally connected has disappeared. The wood from which the photograph was made came from a region of the trunk

more than a foot below the crown, and showed bundles in the fusiform rays through their entire course, even projecting a short distance into the pith (fig. 18). This persistence and continued growth of the leaf traces, together with the connections with the secondary

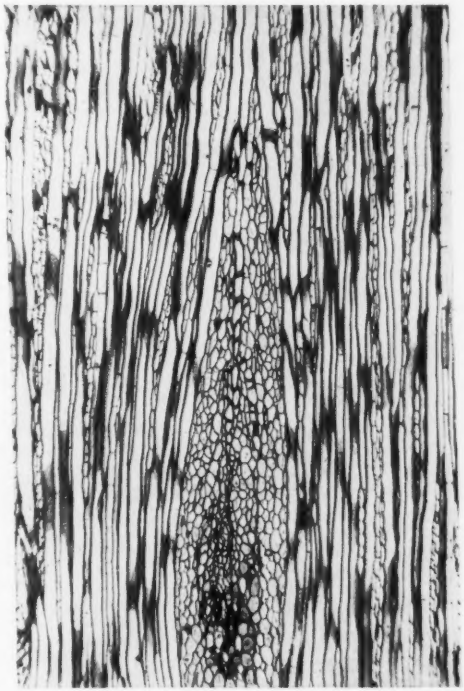


FIG. 3.—Tangential section through mature wood; part of a broad ray occupies middle region, and in it a tracheid may be seen joining the leaf trace with the secondary xylem; ×35.

tracheids, indicate that the traces take on a new function when they cease to supply leaves, namely, the connecting up of the inner and outer layers of wood. In these old leaf traces the xylem is the only part which remains functional. In contrast to the pitted tracheids of the surrounding wood, the traces show only scalariform tracheids, or at most a few elements with transitional stages to the pitted con-

dition. It will be recalled that persistent leaf traces occur also in *Araucaria* and *Agathis*. The cells comprising a ray are usually two or three times as long in the radial direction as in the other dimensions, and are provided with pits which bear some resemblance to sieve plates. Such pits occur abundantly in the cells of pith, cortex, and wood parenchyma (fig. 6), and no doubt serve to facilitate storage and the utilization of stored foods.

PHLOEM.—Three kinds of elements occur in *Microcycas* as in the other genera of cycads: sieve tubes, parenchyma, and fibers. It may be seen in fig. 5 that the radial rows of phloem cells are separated by the somewhat wider cells of the rays, that the hard and soft elements of the bast are mixed without rule, and that the proportions of hard and soft elements vary in different regions. The preservation of the phloem in the material collected at Consolacion is particularly good, and has made it possible to secure satisfactory preparations of the soft bast. Like the tracheids, the sieve tubes are on a liberal scale, having a diameter of 35 μ in many cases, although some are only half that width. The sieve plates show very clearly when stained in iron-alum haematoxylin, and are shown in figs. 19 and 21. The sieve plate typical of cycads is found where two sieve tubes are in contact in the tangential plane, hence is best seen in radial sections. It differs essentially from the sieve plate of ferns on the one hand and conifers on the other. It is perhaps safer to speak of sieve areas than sieve plates, for the area covered by pores may extend for a considerable distance with slight interruptions, especially in the reproductive axis (fig. 22). On account of the width of the sieve tubes, the sieve areas are apt to be large, and their horizontal extent is greater than the vertical, but there is great irregularity in their size and shape, and they show a distinct tendency to be bunched. The pores are smaller but much more numerous than is the case in a fern such as *Pteris*. A second type of sieve plate occurs where a sieve tube comes into contact on its radial face with a fiber or parenchyma cell. As seen in fig. 19, it is a smaller and more diffuse group of pores, giving the effect of a general speckled wall, the speckles however being more or less grouped. Rather similar groups of pores occur in great numbers on the walls of the parenchyma cells, including the ray cells, in which the pores are quite conspicuous.

This porous condition is found also in the part of the ray traversing the xylem, as has already been mentioned, and is represented even in the fundamental tissue, especially of the cortex. Such pitting has been reported for the ray cells of a number of dicotyledons (10).

The form of the parenchyma cells of the phloem is clearly shown in fig. 19. They are found associated with the sieve tubes, but there appears to be nothing definite about their arrangement. Some of them contain considerable starch, while others are entirely devoid of it. STRASBURGER (18) considered that these starch-free cells function as companion cells, and this may be the case, although there is no difference in form or position between these and the regular storage cells of the phloem.

The fibers of the phloem are a conspicuous feature, on account of their great number and thick walls. In the earliest formed phloem they are relatively scarce, but in the later formed layers they are much more abundant than the elements of the soft bast. Old stems in fact show a phloem made up almost entirely of fibers in the later layers. The sparsity of fibers in the early phloem is probably to be regarded as reminiscent of the ancestral condition, for in those Cycadofilicales in which the phloem is preserved (*Heterangium tiliaeoides*, *Lyginopteris*, *Medullosa*, *Cycadoxylon Fremyi*, 15) no thick walled bast elements have been found. A peculiar feature of the fibers of *Microcycas* is the large proportion of cellulose contained in their secondary walls, while the middle lamella contains a moderate amount of lignin, as indicated by the phloroglucin test. MILLER (12) describes the fibers of *Cycas media* as suberized, but unfortunately he does not state the microchemical reaction upon which this statement is based. CHAMBERLAIN has very kindly placed at my disposal some material of the stem of *Cycas media*. In this material, as in corresponding material of *Microcycas*, the following reactions occur: the secondary thickening of the phloem fibers (1) turns violet with zinc chloriodide, (2) turns deep blue with iodine and sulphuric acid, (3) dissolves in cuprammonium. For these reasons it may safely be inferred that cellulose is the predominant substance in the thick secondary walls of these fibers.

PITH BUNDLES.—The pith of the stem usually shows no vascular bundles, although in the neighborhood of the vascular ring in older

parts of the trunk small groups of tracheids may frequently be seen, having been detached from the main mass of xylem by reason of late growth of fundamental tissue cells. Occasionally, however, there may occur a short distance inward from the protoxylem a bundle with inverse orientation. The bundle shown in fig. 20 has half a dozen scalariform and pitted tracheids, a conspicuous cambium, and a phloem made up of hard and soft bast. Whether the sporadic occurrence of such bundles should be regarded as significant is open to question, but it will be recalled that the Medullosae, generally considered to be the probable ancestors of modern cycads, had concentric bundles, while *Lyginopteris Oldhamia* frequently exhibited the feature of pith bundles with inverted structure, and such a phenomenon was excessively developed in the different species of *Cycadoxylon*. SCOTT (17) reports the occurrence of similar strands in the peduncle of *Stangeria*. The finding of bundles with inverse arrangement of tissues in *Microcycas* may add one more item to the accumulation of evidence for the medullosan origin of the cycads.

Root

Like the stem, the root contains much parenchymatous tissue, but here it is located almost wholly in the cortex. Apparently the root grows very slowly in thickness. All of the roots examined were triarch, although DORETY (7) found tetrarch structure, "with a reduction to triarch toward the tip, in some cases" in her material of the seedling. Such variations are common in other plants. The primary xylem consists of spiral and scalariform elements of the same general type as is found in the stem, but the secondary xylem is almost entirely of the pitted sort. We have here an additional argument for considering the pitted tracheid to be the ancestral type, in view of the well known conservative tendency of the root. Bast fibers have a relatively poor development. Mucilage canals are absent.

Leaf

The main features of the structure and course of the leaf trace bundles of cycads have been familiar since the classic work of METTENIUS (11), who traces in *Cycas* and *Dioon* the change from endarch to mesarch, and finally a close approach to exarch struc-

ture. Recently THIESSEN (**19**) has made a careful study of the cotyledonary traces of *Ceratozamia*. *Microcycas* presents a few features of interest. In the greatly swollen base of the petiole the bundles have lost the greater part of the centrifugal xylem which they possess in the cortex, and have taken on a great amount of centripetal xylem which here forms a U-shaped mass (fig. 12). In contact with each arm of the U, and also with the centrifugal elements of the primary xylem, is a well developed mass of secondary xylem, showing rays as well as tracheids. As the bundles pass outward into the petiole proper, they quickly lose all of their secondary wood, and all but a few elements of the centrifugal xylem, while the centripetal wood becomes a somewhat rounded mass constituting from here onward the bulk of the xylem. One of the bundles from the lower third of the rachis is shown in fig. 13, from which may be seen the very small amount of centrifugal xylem (restricted in this bundle to two tracheids), also the absence of secondary xylem, although several layers of the phloem have the radial arrangement. The longitudinal view (fig. 8) shows a more typical protoxylem than is found in the stem, made up of long spiral elements which have become torn by the elongation of the rachis. The centrifugal xylem is represented in this case by a single narrow tracheid with scalariform thickening, and is separated from the protoxylem by a band of parenchyma, as has been observed in other genera. The centripetal xylem presents a series of wide spiral, scalariform, and transitional elements. The pitted condition characteristic of the tracheids of the stem is scarcely reached, and the scalariform tracheid is decidedly the typical one. Comparing fig. 8 with BAILEY'S figure of the corresponding region of *Ceratozamia*, it will be seen that *Microcycas* lags behind *Ceratozamia* in this regard. The occurrence of pitted tracheids in the petiole of cycads may be taken to indicate that there were such elements in the primary wood of the forerunners of this group. This implication is in fact borne out by the fact that the primary xylem of *Medullosa* consists in part of pitted tracheids. In view of these considerations, the persistence of scalariform tracheids for some distance out in the secondary wood of *Microcycas* appears all the more remarkable, and is probably to be interpreted as the persistence of a juvenile feature which in geophilous cycads, such

as *Zamia*, lasts throughout the life of the plant. The only conspicuous feature of the phloem of the petiolar bundles is the almost total absence of the bast fibers so abundant in the stem. Many of the bundles show no fibers whatever, while other bundles containing as many as 100 phloem elements show one, two, or at most three bast fibers. This is in accord with the conservative tendency of the leaf. Each of the numerous veins which traverse each leaflet contains a bundle built on the same general plan as those of the petiole but much smaller, and surrounded by a sheath containing elements of two sorts: thick walled fibers with dense contents, and fairly thin walled empty looking cells, which certainly fit in with WORSDELL's description applying to leaflets containing numerous bundles: "inconspicuous and scarcely recognizable as transfusion tissue such as it is seen in *Cycas*" (**20**). The cells in question show no bordered pits nor reticulate markings, and would probably pass unnoticed if the striking condition in *Cycas* had not already been observed. In passing it may be mentioned that the leaflets of *Microcycas* generally fall off in the process of drying, in which respect they differ from the leaflets of *Zamia* and other genera.

Cone axis

The vascular tissue of this region does not form a continuous cylinder as is the case in the stem, but consists of a circular row of bundles. Unlike the leaf traces, these bundles show a liberal amount of secondary tissue, with distinct rays and a large proportion of phloem, which, however, is entirely devoid of fibers (fig. 10). In accordance with the greater food transport to the megasporangiate cone, its phloem is extremely well developed, with very numerous wide sieve tubes having the sieve areas so extensive as nearly to cover the radial walls (fig. 22), while the woody part of the bundle is more or less broken up into narrow strips separated by wide rays. The entire absence of pitted tracheids in either of the cones is to be remarked; only spiral and scalariform elements have been observed. The protoxylem elements are at the tip of each wedge-shaped mass of xylem, in sharp distinction from the condition in the leaf bundles. SCOTT (**17**) has described for *Stangeria* and three other genera a small amount of centripetal xylem in the bundles of the peduncle. A

search for these elements has been made in *Microcycas*, and they appear not to be nearly so well developed as in *Stangeria*, although present to the number of two or three scalariform tracheids in bundles of the stalk of the microsporangiate cone, as shown in figs. 9 and 11. These tracheids are short and interrupted, and perhaps for this reason none can be found in some of the bundles. SCOTT speaks of the shortness of similar tracheids in *Stangeria*, and attributes it to their comparatively late development. They are separated from the rest of the xylem by a few wide parenchymatous cells. None have so far been observed in the megasporangiate cone, nor in the axis of the cone itself. It is interesting to note that it was the microsporangiate cone in which SCOTT found the best showing of centripetal wood in the case of *Stangeria*. A few cases of horseshoe-shaped and of truly concentric bundles have been found in the cortex of the peduncle of the megasporangiate cone. Particularly plain cases of centripetal xylem occur in the stalk of the megasporophylls. From three to five bundles run up through this stalk, and these small bundles generally show several centripetal tracheids whose walls are provided with scalariform thickenings like those of the centrifugal portion of the xylem. The amount of centripetal xylem in these bundles appears to be as great as that figured by WORSDELL (**21**) in the case of *Stangeria* and *Dioon*.

Discussion

When *Microcycas* was first studied, the suggestion was made by CALDWELL that it "may be regarded as the most primitive cycad yet described" (**2**). The investigation of its histology ought to throw some light on this question. The concept "primitive species" has of late been reinterpreted in accordance with the doctrine of conservative organs advocated by English anatomists and emphasized by the work of JEFFREY (**8**). Since the various organs or regions of a plant differ in conservatism, and since one supposedly conservative organ may lag behind others of the same plant, a primitive species has come to mean one in which primitive characters predominate either in number or supposed significance. For instance, the extreme conservatism of the megasporophyll of *Cycas* might be rated more highly than the character of the vernation. A discussion

of relationships might naturally lead to a consideration of all the genera, but such is outside the scope of the present paper. We shall rather point out certain of the criteria which have been advanced for determining the position of cycad genera, and apply these criteria to *Microcycas*.

The basis upon which *Microcycas* was regarded as primitive by CALDWELL is undoubtedly the large number of sperms produced in the male gametophyte. This number exceeds even that produced by a fern antheridium. Related to this point is the exceedingly large number of archegonia, a feature regarded by CHAMBERLAIN as a highly specialized one. The embryogeny is still imperfectly known in this genus, and so furnishes no basis for comparison. The number of cotyledons was earlier (**2**) stated to be three to six, but DORETY (**7**) finds the usual number to be two, thus bringing this genus in line with the other genera. The fact that the microsporangia are scattered over the face of the sporophyll, instead of being arranged in sori, is probably to be regarded as an advanced feature. The peltate form of the megasporophyll, lacking any semblance of leaf form, would place the genus very close to *Zamia*, which is considered by CHAMBERLAIN (**6**) to be the most highly specialized genus in this respect.

Passing on to the vegetative organs, *Microcycas* belongs to the group of genera possessing a definite trunk. The fact that the cycads of earlier periods appear at any rate not to have had merely a subterranean stem or caudex would indicate that genera such as *Stangeria* and *Zamia* have secondarily assumed this habit, and that the treelike habit is to be regarded as ancestral. Another gross character is the marked persistence of the leaf bases, extending over many years. This may be taken to be the continuance of an early habit. Two leaf characters may stand as criteria, one being the vernation, which in *Microcycas* shows no indications of a fern ancestry. Moreover, the general habit of the leaf is less fernlike than some other genera, for instance *Stangeria*.

Coming to the internal structure of the plant, the single vascular cylinder of the stem is to be noted, in sharp contrast to the polyxylic habit of *Cycas* and *Macrozamia*. If the current view that *Medullosa*

is ancestral to the cycads be adopted, the monoxylic habit would stand as a feature of reduction. Another significant feature of *Microcycas* in common with the other arboreal genera is the pitted tracheid as the characteristic unit of the mature xylem, contrasting with the scalariform tracheid occurring exclusively in the stem wood of *Stangeria* and *Zamia*. Inasmuch as the fossil genera *Cycadoxylon*, *Lyginopteris*, *Heterangium*, and *Medullosa* show a xylem made up of pitted tracheids, this feature may be regarded as ancestral. A closely connected feature is the pronounced slowness with which the mature condition characterized by pitted tracheids is reached; it has been pointed out that a broad zone of scalariform elements precedes the mass of pitted tracheids. A comparative study of the genera from this point of view remains to be made. It is typical of cycad leaves to have the centripetal xylem strongly developed; in *Microcycas* the centrifugal elements of the primary wood are very few, and may even be absent. We see here the culmination of a movement beginning in some ancestor with a clearly mesarch leaf trace. The prevalence of scalariform and transitional elements in the primary xylem of the leaf can hardly be regarded as pointing to a primitive condition, in view of the presence of undoubted pitted tracheids in the petioles not only of *Cycas* but even of *Zamia*, a genus in which none of these elements occurs in the stem. The scarcity of centripetal xylem in the cone axis of *Microcycas*, compared with *Stangeria*, does not indicate a particularly low place in the list for the former genus. The centripetal tracheids appear to be in their last stages of disappearance, as would be appropriate to a truly advanced genus. The occurrence of scalariform and not pitted tracheids in the cone may point to a remote ancestor, but we are not in a position to contrast the other genera of cycads in this particular. The same may be said with regard to the scarcity of phloem fibers in the primary phloem of the stem and in the leaf traces, and the entire absence of these fibers in the cone axis.

Taking the various criteria into consideration, it would appear that *Microcycas* is far from the bottom of the list of genera, although it may be regarded as less specialized than such a subterranean genus as *Zamia*, to which it apparently stands close.

Summary

1. An extension of the range of *Microcycas* is noted, recording the occurrence of a station on the lowlands.

2. The trunk differs from that of *Dioon* in having conspicuous and persistent external rings composed of leaf bases separated by wider spaces occupied by scales.

3. The xylem of the stem consists typically of pitted tracheids, but there is a remarkably wide inner zone of scalariform elements representing a juvenile stage.

4. The scalariform zone shows some indication of division into a few growth rings.

5. Protoxylem is definitely present in the stem. It is endarch, and consists of narrow tracheids with close spiral and reticulate thickenings, followed by scalariform elements of increasing diameter.

6. The leaf traces are persistent, and become secondarily attached to the later formed tracheids of the woody cylinder, establishing a connection between the inner and outer wood.

7. The phloem of the different organs varies as to presence of bast fibers. A phylogenetic significance is attributed to this.

8. Pith bundles with inverse orientation occur sporadically.

9. A small amount of centripetal xylem is found in the peduncle of the microsporangiate cone.

10. A consideration of the various features leads to the conclusion that *Microcycas* is a distinctly advanced genus.

RUTGERS UNIVERSITY
NEW BRUNSWICK, N.J.

[Accepted for publication January 25, 1926]

LITERATURE CITED

1. BAILEY, I. W., Some salient lines of specialization in tracheary pitting. I. Gymnospermae. Ann. Botany **39**:587–598. 1925.
2. CALDWELL, O. W., *Microcycas calocoma*. BOT. GAZ. **44**:118–141. 1907.
3. ———, A study of *Microcycas calocoma*. 2d. Rept. Estacion Cent. Agronom. de Cuba. *122–132*. 1909.
4. CALDWELL, O. W., and BAKER, C. F., The identity of *Microcycas calcoma*. BOT. GAZ. **43**:330–335. 1907.
5. CHAMBERLAIN, C. J., The adult cycad trunk. BOT. GAZ. **52**:81–104. 1911.
6. ———, *The living cycads*. Chicago. 1919.

7. DORETY, HELEN A., Vascular anatomy of the seedling of *Microcycas calocoma*. BOT. GAZ. **47**:139–147. 1909.
8. JEFFREY, E. C., The anatomy of woody plants. Chicago. 1917.
9. LANGDON, L. M., Stem anatomy of *Dioon spinulosum*. BOT. GAZ. **70**:110–125. 1920.
10. MACDANIELS, L. H., The histology of the phloem in certain woody angiosperms. Amer. Jour. Bot. **5**:347–378. 1918.
11. METTENIUS, G., Beiträge zur Anatomie der Cycadeen. Abh. Math.-Phys. Classe Königl. Sächs. Gesells. Wissensch. **5**:567–608. 1861.
12. MILLER, W. L., Polyxylic stem of *Cycas media*. BOT. GAZ. **68**:208–221. 1919.
13. PENHALLOW, D. P., A manual of the North American gymnosperms. Boston. 1907.
14. RECORD, S. J., Economic woods of the United States. New York. 1912.
15. RENAULT, B., Bassin houiller et permien d'Autun et d'Epinac. Flore Fossile, Part 2. 1896.
16. SCOTT, D. H., Studies in fossil botany. London. 1900.
17. ———, The anatomical characters presented by the peduncle of Cycadaceae. Ann. Botany **11**:399–419. 1897.
18. STRASBURGER, E., Histologische Beiträge. III. Jena. 1891.
19. THIESSEN, R., The vascular anatomy of the seedling of *Dioon edule*. BOT. GAZ. **46**:357–380. 1908.
20. WORSDELL, W. C., On "transfusion-tissue"; its origin and function in the leaves of gymnospermous plants. Trans. Linn. Soc. II. **5**:301–319. 1897.
21. ———, The vascular structure of the sporophylls of the Cycadaceae. Ann. Botany **12**:203–241. 1898.
22. ———, Comparative anatomy of certain species of *Encephalartos*. Trans. Linn. Soc. Bot. **4**:445–457. 1899.

EXPLANATION OF PLATES XVI–XVIII

PLATE XVI

FIG. 4.—Transverse section through xylem of stem; edge of one of the broad rays appears at left; ×110.

FIG. 5.—Transverse section through phloem of stem; earlier formed phloem at upper side, marked by relatively few fibers; ×110.

FIG. 6.—Radial section through mature xylem of stem; at left a row of parenchyma cells, showing many small pits; ×120.

FIG. 7.—Radial section through transition region of xylem; stray starch grain appears in one of the tracheids; parenchyma at right; ×170.

FIG. 8.—Longitudinal section through xylem of bundle of petiole; at right a scalariform element belonging to centrifugal wood; ×230.

FIG. 9.—Longitudinal section through xylem of bundle from peduncle of microsporangiate cone; at left a few centripetal tracheids, followed by protoxylem; ×140.

PLATE XVII

FIG. 10.—Transverse section through bundle of peduncle of microsporangiate cone; ×75.

FIG. 11.—Part of bundle shown in fig. 10; near large tannin-filled cell are two tracheids belonging to centripetal wood; ×115.

FIG. 12.—Transverse section through bundle in swollen basal region of petiole; U-shaped primary xylem in contact with secondary xylem; ×115.

FIG. 13.—Transverse section through bundle of lower third of rachis; secondary wood has disappeared, and only a few centrifugal tracheids present; ×120.

FIG. 14.—Transverse section through tip of xylem wedge next to pith of stem, showing position and appearance of protoxylem; ×130.

FIG. 15.—Similar view, but through older part of stem, showing separation of tip region of xylem through growth of fundamental tissue cells; ×70.

PLATE XVIII

FIG. 16.—Tangential section through inner region of xylem of stem; tracheids have scalariform thickenings on all faces; ×85.

FIG. 17.—Tangential section through outer region of xylem of stem; tracheids have bordered pits on radial walls; rays and parenchyma also shown; ×85.

FIG. 18.—Transverse section through inner region of xylem of stem, showing in one ray a bundle which projects into pith; ×35.

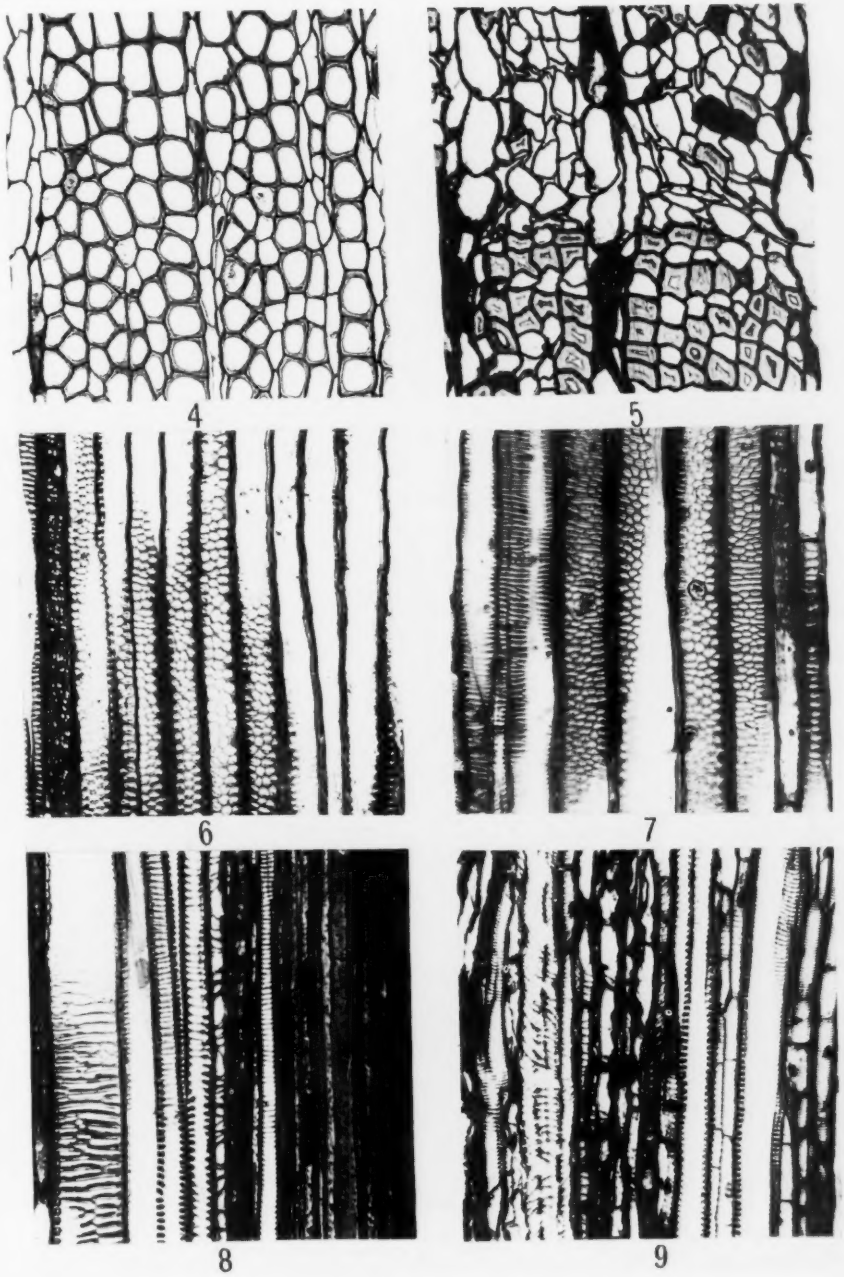
FIG. 19.—Radial section through phloem of stem; at left are sieve plates of type occurring where two sieve tubes are in contact; at right is type of sieve plate occurring where a sieve tube touches a parenchyma cell; ×200.

FIG. 20.—Transverse section through pith bundle having inverse orientation; ×40.

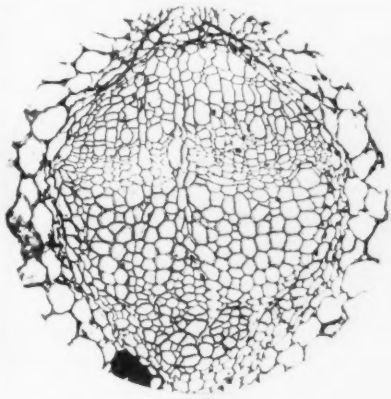
FIG. 21.—Another view of sieve plates found in stem; ×200.

FIG. 22.—Longitudinal section through phloem of bundle of peduncle of microsporangiate cone; the wide sieve tube shows extensive sieve areas; ×120.

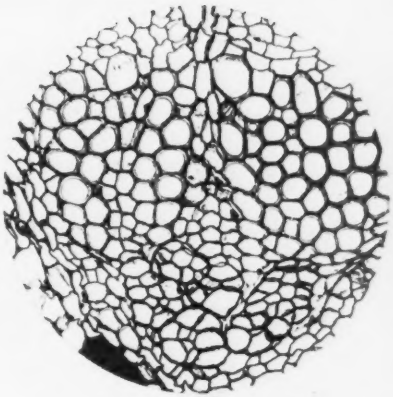
FIG. 23.—Tangential section through protoxylem of stem, showing close spiral thickenings characteristic of tracheids in this region; ×275.



CHRYSLER on MICROCYCAS

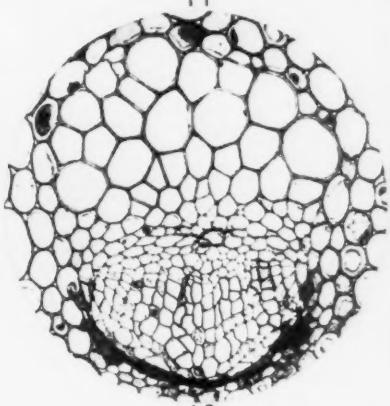


10

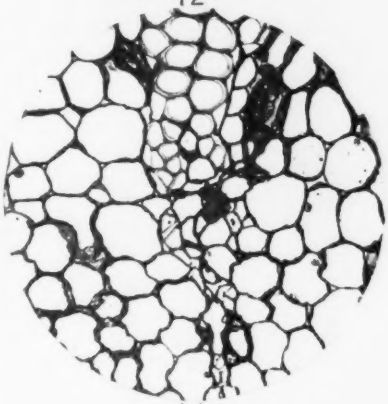


11

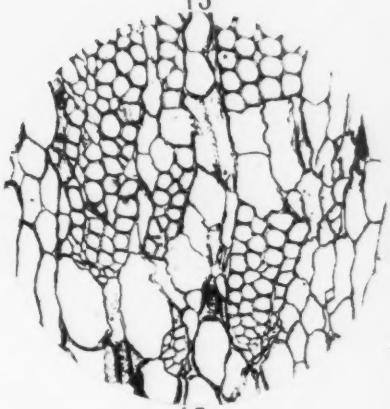
12



13

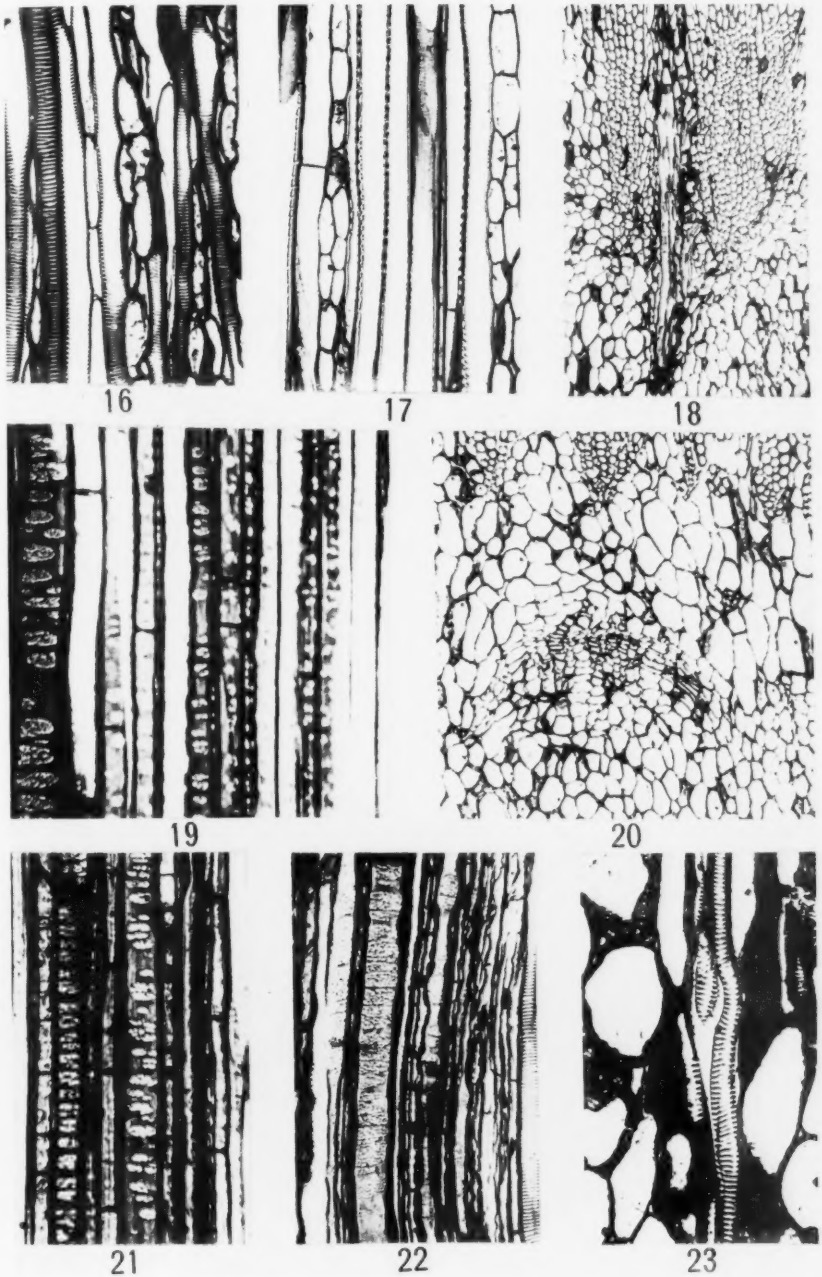


14



15

CHRYSLER on MICROCYCAS



CHRYSLER on MICROCYCAS

AN ECOLOGICAL STUDY IN UTAH

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 356

P. ALICE EVANS

(WITH FOURTEEN FIGURES)

Introduction

The region described in this paper comprises the greater portion of Salt Lake County, Utah, excluding in the west the foothills and mountains of the Oquirrh Range, and in the east three canyons (Mill Creek, Parleys, and Red Butte) of the Wasatch Range. This region offers so much topographical, geographical, geological, and botanical variety that it appeared to present unusual opportunities for a study in plant ecology.

Situated on the eastern boundary of the Great Basin, having within its confines Great Salt Lake, and provided by reason of the Wasatch fault with high mountain ridges down which mountain streams (aided in some instances by glacial action) have cut steep canyons, there is found here within a comparatively small area a wide variation in altitude, soil conditions, precipitation, and climate.

The region studied can be divided into two very contrasting portions: (1) the Salt Lake Valley, extending westward from the foothills of the Wasatch Range to the southwestern shores of Great Salt Lake; and (2) the mountainous area from the foothills up four of the main canyons to the crest of the Wasatch Range, which forms the eastern limits of the county. Both of these areas are bounded on the north and south by the county lines. The map of Salt Lake County (fig. 1) shows the area studied.

The valley and mountain bases were at one time part of Lake Bonneville, which existed in the Great Basin area (3) during the Quaternary period (fig. 2). The shore levels of Lake Bonneville extended 1000 feet above the level of its remnant, the present Great Salt Lake. The soils in the valley are those typical of water deposition, and are of considerable depth. Just north of the county, wells drilled 2000 feet deep still encounter this lacustrine material (9).

The various hypotheses concerning the nature of Lake Bonneville mostly contend that it was alternately fresh and alkaline during its periods of oscillations. The shore levels which clearly show on the slopes of the adjacent mountains are proof enough of this. The fine character and the variation in the amounts of deposition caused

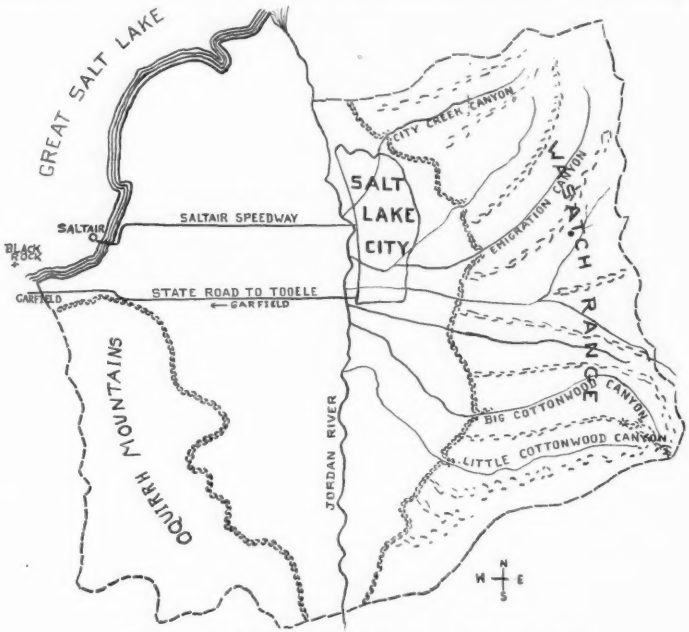


FIG. 1.—Salt Lake County, Utah, showing area studied

GILBERT (6) to believe that the chemical content of the water varied, causing during the different levels of the lake different degrees of soil and salt precipitation. As desiccation took place the chemical constituents increased, and their ultimate deposition and concentration resulted in the alkali lands and the present Salt Lake. KEYES (7) thinks that the fine depositions are of an aeolian nature; that is, the dust carried in from the arid southwest would settle on the lake surface and gradually be deposited at the bottom, there to remain. Desiccation would account for the present alkalinity of lands and water.

Both prior to and synchronous with the periodic oscillations of Lake Bonneville were periods of glaciation in the high Wasatch Mountains. The morainic deposits which occur along the sides and near the mouths of some of the glaciated canyons give evidence that there were at least two glacial epochs here. Portions of the outer morainic drifts are buried under beds of sand and gravel. The

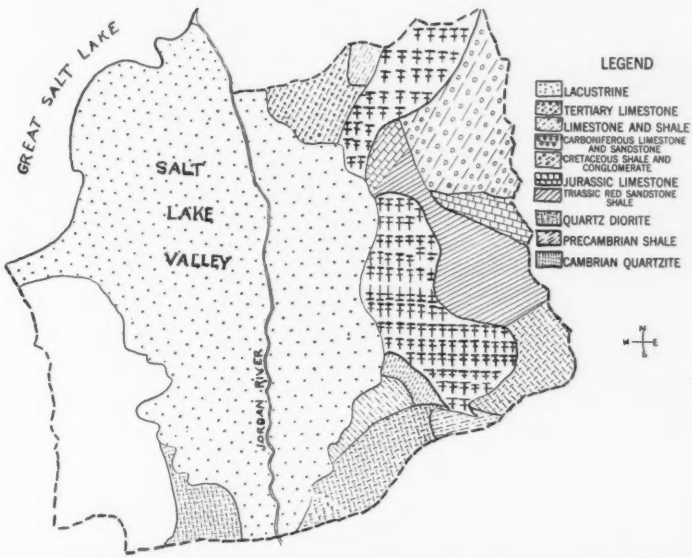


FIG. 2.—Geologic map of Salt Lake County, adapted from U.S. Geologic Map IV in *The ore deposits of Utah* by BUTLER, LAUGHLIN, and others. Professional Paper III of U.S. Geol. Survey. 1920.

burial of the earlier drift by lacustrine material indicates clearly that they are at least pre-Bonneville in age. The older deposits have disintegrated so much more than the later deposits, that it is supposed that the interglacial epoch must have been longer than the postglacial epoch. ATWOOD (1) states:

> Furthermore, the outer moraines above the Bonneville shore have suffered much erosion. They are softened in contour and somewhat dissected, whereas the inner moraines are fresh in topographic appearance as well as in the condition of their material.

This also shows that the ice of the earlier epoch was more extensive than that of the later.

Since Quaternary times the temperature has increased and humidity decreased, causing the lake and glaciers nearly to disappear. Most of the canyons of the region of the Wasatch Range have large streams, which since the retreat of the lake and ice have eroded gorges in the morainic drifts and through the lake shore terraces, and formed in some instances rather large deltas at their mouths.

The purpose of the investigation recorded in this paper was to study the narrow strip of the Great Basin area included in Salt Lake County, Utah, and the adjacent canyons in the western Wasatch Range as to geological formation, and also as to the vegetational cover, including the effect thereon of climatic and other local modifying factors. The canyons selected for this study were four, two of which are representative of the main glaciated area of this region, namely, Big Cottonwood and Little Cottonwood canyons, while the others, Emigration and City Creek canyons, are unglaciated.

The discussion of this study will be made in the following order: (1) the lowland or Salt Lake Valley; (2) the unglaciated canyons; and (3) the glaciated canyons.

Salt Lake Valley

The valley as shown on the maps is divided by the Jordan River into an east and a west portion. The Jordan River rises in Utah Lake, a body of fresh water about 10 miles south of Salt Lake County, flows north through the county, and empties into Great Salt Lake.

The soil of the valley has had a common origin, namely, that of a lacustrine deposition, but there is now a great difference in chemical composition between the soil on the west side of the Jordan River and that on the east side. This is doubtless due to the fact that the fertile soil on the eastern side consists largely of eroded material from the mountains, which has been prevented from reaching beyond the Jordan River because the river flows parallel to the base of the mountains. The examination of the valley section, therefore, has naturally been divided into two very different areas, based

on soil composition: (1) the land west of the Jordan River extending to Great Salt Lake, which area, excepting a narrow strip of land about 2 miles in width adjoining the river and some land south of the Garfield Road near the base of the Oquirrh Range, is of an alkaline nature and decidedly unfertile (11); and (2) the land east of the Jordan River extending to the foothills of the Wasatch Range, which is very fertile if water is available.

Logically the beginning of the study is in the western area, on the shores of Great Salt Lake. Fig. 3 shows the most western point of study in the region of Black Rock, an isolated granite post standing in the water about 70 feet from the railroad, and used only as a landmark. Here the shore of the lake has been greatly modified, due to the construction of the Western Pacific Railroad. Wooden piling driven along the margin of the lake is filled with rocks, thus separating the main body of water from the marshes that lie at the base of the limestone cliffs of the Oquirrh Range, which here reaches its northern limit. The study here dealt with the vegetation around the marshes and on the tops of the cliffs, and is recorded as follows:[1]

Marshes	Vegetation on dry cliffs
Alopecurus fulvus	Asclepias speciosa
Atriplex confertifolia	Ascerates viridiflora linearis
Abronia salsa	Achillea millefolium
Distichlis spicata	Atriplex confertifolia
Iva axillaris	Atriplex canescens
Phragmites communis	Bromus tectorum
Ranunculus Cymbalaria	Monothrix Stansburijii
Salix fluviatilis	Malvastrum coccineum
Sesuvium sessile	Sarcobatus vermiculatus
Sarcobatus vermiculatus	Salsola pestifer
Salsola pestifer	Eurotia lanata
Trifolium longipes	

About one mile east of Black Rock the railroad turns inland, leaving the shore line undisturbed. Here is a bare sand beach, irregular in width due to the oscillations of the lake level, which is stationary only when rainfall and inflow equal evaporation. This is not often the case, as will be shown in the discussion on the climatic

[1] The names follow the nomenclature of Coulter and Nelson (4); in a few instances they were obliged to be taken from Garrett (5) and Rydberg (10).

conditions of the region. Also wind storms cause variation in the advance of water, which is marked by drift wood and dead vegetation. The plant that here ventures nearest the water's edge is *Distichlis spicata*. Associated with it, near the zonal margin away from the lake, are to be found *Juncus balticus* and *Alopecurus fulvus*. Just behind this salt grass area is a raised beach which might be termed a foredune. On this raised portion are to be found such plants as *Anogra cinerea*, *Asclepias speciosa*, *Sporobolus airoides*, *Chrysothamnus graveolens glabrator*, *Iva axillaris*, and *Kochia vestita*.

FIG. 3.—Shore of Great Salt Lake and Black Rock at Garfield, Utah

Just south of the foredune are moist depressions and brackish marshes, the banks of which are inhabited by *Typha latifolia*, *Juncus balticus*, *Phragmites communis*, *Salix fluviatilis*, *Atriplex confertifolia*, and *Distichlis spicata*, which still grows here where not crowded out by other vegetation.

These three vegetational zones paralleling the lake shore line continue eastward only a short distance. They are again interfered with by a slag dump from the Garfield smelter, which is situated on the north-facing foothills of the Oquirrh Range. This disturbed area was not studied, it being plantless in the main.

The study was taken up again on the eastern shore of the lake near the Saltair Resort (fig. 1). Here there is a large plantless beach which is of a very miry nature, covered by a heavy deposit of alkali salts, algae, and larva cases of Ephedra fly. This is a most unpleasant beach to look upon, and if the material is disturbed the resulting

odor is equally unpleasant. As the substratum becomes firmer it is occupied by a scant stand of *Allenrolfia occidentalis*, *Salicornia utahensis*, and *S. rubra*, which are the most salt-tolerant plants of this region. Just east of this area is a less alkaline zone, which, with the exception of the commercial salt fields that occupy a considerable area, is covered by a sparse vegetation, the dominant plants being *Atriplex confertifolia*, *Distichlis spicata*, *Chenopodium salinum*, *C. rubrum*, *Sarcobatus vermiculatus*, *Salsola pestifer*, and *Kochia vestita*. This type of vegetation, excepting in the vicinity of the salt fields, covers the greater portion of the lower and level areas west of the Jordan River and north of the Garfield automobile road, comprising in all about 125 square miles. On the higher areas are to be found *Kochia vestita*, *Grayia spinosa*, *Poa Sandbergii*, and *Sphaerostigma pubens;* while on the crest of these raised areas are *Artemisia tridentata*, *Gutierrezia Sarothri*, *Erodium cicutarium*, and *Bromus tectorum*.

The land adjacent to the river and south of the Garfield road is in the main higher than that just described, and the alkali, if it was ever present, has been drained away. In the natural condition these higher benches are covered by a growth of *Artemisia tridentata*, *Chrysothamnus nauseosus albicaulis*, and various annuals and grasses. Along the river are also found *Salix fluviatilis*, *Rosa Nutkana*, *Apocynum* sp., *Acer Negundo*, and tall herbaceous plants such as *Rumex crispus*, *Chenopodium album*, and *Urtica* sp.

Most of this river bench and south portion of the land west of the Jordan River is of fair agricultural value, and has successfully been cultivated for several decades. The crops in the main are alfalfa and sugar beets, with some garden truck. There are also a few orchards.

The northern and alkali region to be of any agricultural value must be drained. It is an excess of sodium carbonate or black alkali which is the principal obstacle here. Even converting this by the use of gypsum into white alkali would still leave an excess of salts in the soil, so that drainage seems to be the only feasible solution of the problem. During the last few years attempts have been made to reclaim portions of the alkali land by the construction of drainage canals. About 90 square miles are said to be capable of reclamation in this manner.

The land east of the Jordan is about 4450 feet above sea level, and is 230 feet higher than the shore of Great Salt Lake. The gradient is rather steep and merges into the foothills of the Wasatch Range. Where water from the Jordan River and from the Canyon streams has been available for irrigation, crop cultivation has been carried on. The land is very fertile, and the climate favorable to such crops as peaches, apricots, cherries, and apples; small fruits in abundance, such as currants, gooseberries, raspberries, and strawberries, and many kinds of melons are also grown.

The large streams from the canyons have produced rather large deltas, especially City Creek and Big and Little Cottonwood Canyon streams. Salt Lake City occupies all of the City Creek delta and the adjacent benchland to the north and east. The other deltas are occupied mainly by farm land. The lowlands between are mostly meadow and are ideal for dairy farms. The virginal stand of vegetation has long since disappeared from this side of the valley, due to the extensive agriculture on the lower lands and the overgrazing of the benchlands by sheep and cattle. Even as early as 1875, during the Powell Geological Survey, GILBERT (6) observes:

> In the virgin condition most lowland valleys and all of the upland valleys were covered by grass and other herbaceous vegetation. These have been eaten off by the herds of the white man and in their place has sprung up a sparse growth of low bushes between which the ground is bare.

However, although this area has been overgrazed and also burned over frequently and otherwise modified by man, there still remains a great differentiation between the lowland and benchland flora. Individual owners have protected certain areas, so that we can get some idea of the probable original vegetational cover of the east valley under these divisions: (1) the lowlands which are of three types (marshlands, drylands, and the vegetation along the stream banks); (2) the benchlands, including protected and unprotected areas. The vegetation is listed under these headings in the table.

LOWLANDS

LOW MARSHLANDS	LOW DRYLANDS (TREELESS AREAS)
Acer Negundo	Purshia tridentata
Populus angustifolia	Chrysothamnus nauseosus
Salix Scouleriana	Grindelia squarrosa

LOWLANDS—*Continued*

Low marshlands	Low drylands (treeless areas)
Typha latifolia	Malva rotundifolia
Sagittaria arifolia	Phlox longifolia
Equisetum hiemale	Erodium cicutarium
Equisetum arvense	Linum Lewisii
Scirpus lacustris	Bromus tectorum
Juncus balticus	Calochortus Nuttallii
Sium cicutaefolium	Delphinium Nelsonii
Camassia esculenta	Lepidium perfoliatum
Brodiaea Douglasii	Capsella Bursa-pastoris
Valeriana ceratophylla	Draba caroliniana
Viola Howellii	Glycyrrhiza lepidota
Ranunculus Macounii	Viola venosa
R. sceleratus eremogenes	Viola Beckwithii
Onagra strigosa	Convolvulus arvensis
Sisyrinchium angustifolium	Phacelia linearis
Rumex venosus	Lappula subdecumbens
Mimulus Langsdorfii	

STREAM VEGETATION IN VALLEY

Populus angustifolia	Rhus trilobata
Salix lutea	Rosa Nutkana
Salix amygdaloides	Acer Negundo

BENCHLANDS

Protected areas (mainly shrubs with sparse undergrowth of grass and annuals)	Unprotected areas
Purshia tridentata	Achillea millefolium
Chrysothamnus graveolens	Astragalus utahensis
Artemisia tridentata	Grindelia squarrosa
Quercus Gambellii	Wyethia amplexicaulus
Erodium cicutarium	Balsamorrhiza sagittata
Bromus tectorum	Taraxacum officinale
Allium acuminatum	Lithospermum angustifolium
Malvastrum coccineum	Eriogonum ovalifolium
Astragalus utahensis	Lappula subdecumbens
Astragalus cibarius	Phlox longifolia
	Onagra pallida
	Onagra marginata
	Aulospermum longipes
	Opuntia polyacantha
	Viola adunca
	Viola venosa

Unglaciated canyons

City Creek Canyon

Northeast of Salt Lake City is City Creek Canyon, a V-shaped canyon typical of stream erosion, running in a southwesterly direction. The substratum is mainly of limestone with now and then an exposure of trachytic tuffs and breccias, indicating surface volcanic action in the lower part of the canyon (9). Near the head and on the

FIG. 4.—Shrubs growing in depressions on foothills; photograph by SEVILLE FLOWERS.

higher mountain faces are to be found conglomerate and quartzite formations. By comparing figs. 1 and 2 one can see the geologic formations through which the canyon has been eroded.

The vegetation in this canyon has been greatly modified by overgrazing and fire. There are to be found all gradations in succession, from the grass and herb covered foothills through the xerophytic scrub formations to the spruce and aspen forest at the head of the canyon. There is a rise of about 3300 feet from the mouth of the canyon, which is 4450 feet above sea level, to the head of the canyon which is 7800 feet high. In the bottom of the canyon is a rather large stream, one of the main sources of Salt Lake City's

water supply. Along the stream is to be found a vegetation somewhat mesophytic in nature. In this, as in all the canyons studied, the character of the undergrowth changes remarkably with the seasons. In the spring there is a great abundance of ephemerals such as *Claytonia lanceolata*, *Fritillaria pudica*, *F. atropurpurea*, and *Erythronium grandiflorum;* and in the summer and autumn the more xerophytic Compositae and Malvaceae are dominant, with such plants as *Solidago canadensis*, *Senecio serra*, *Helianthus annuus*, *Malvastrum coccineum*, *Malvastrum coccineum dissectum*, and *Sphaeralcea rivularis*.

On the foothills near the mouth of the canyon, as on the unprotected benchlands of the valley, only shortlived grasses and herbaceous plants can grow. The foothills and lower ridges are burned over annually, making it very difficult for a higher type of vegetation to get started. Such areas entirely free from trees and shrubs are found on the ridges in fig. 4. Nearer the head of the canyon the same conditions still exist on the ridges; but in the depressions, especially on the north-facing slope, shrubs are starting to come in, as is shown in the figure. The isolated groups of shrubs in the depressions start as an *Artemisia tridentata* and *Rhus trilobata* association. Then *Quercus Gambellii* comes in, and the *Artemisia* disappears so that most of the patches are *Quercus-Rhus* associations with some *Ribes aureum*. In the higher patches (fig. 4) *Juniperus utahensis* comes in. The undergrowth in these oak patches is made up of such plants as *Mertensia brevistyla*, *Allium acuminatum*, *Phacelia linearis*, *Hydrophyllum occidentale*, *H. capitatum*, *Erysimum asperum*, and *Berberis repens*.

Higher in the canyon the grass cover is succeeded by an *Artemisia-Chrysothamnus* association. This in turn is succeeded by a *Ceanothus velutinus* and a *Cercocarpus ledifolius* association, with *Juniperus utahensis*, *J. scopulorum*, *Sorbus scopulina*, and *Prunus melanocarpa* coming in on the higher and north-facing slopes. Among the last named plants is also to be found *Populus tremuloides*, which soon dominates. Coming in under its shade are to be found *Picea pungens* and *Abies concolor*, which make up the greater stand of vegetation on the north-facing slope of the canyon. Figs. 5 and 6 show the contrast at the head of the canyon between the south-facing

slope, with a mere sprinkling of conifers, and the north-facing slope, with a much denser stand of conifers mingled with *Populus tremuloides*.

The succession of vegetation along the stream is more gradual, due in all probability to the more mesophytic conditions. The following plant lists illustrate briefly the vegetational succession on both south and north-facing slopes and along the stream, culminating at the head of City Creek Canyon in the scant stand of the forest of spruce and aspen.

VEGETATION OF CITY CREEK CANYON

FOREST OF SPRUCE AND ASPEN

Picea pungens
Abies concolor
Populus tremuloides

UNDERGROWTH SHRUBS

Shepherdia argentea
Prunus melanocarpa
Amelanchier alnifolia
Physocarpus malvaceus
Sorbus scopulina
Sambucus microbotrys
Pachystima Myrsinites

HERBACEOUS UNDERGROWTH

Heuchera parvifolia utahensis
Dicentra uniflora
Actaea arguta
Thalictrum Fendleri
Pyrola secunda (very abundant)
Pteridium mucronata

SOUTH-FACING SLOPE

Juniperus scopulorum
Cercocarpus ledifolius
Ceanothus velutina
Cowania mexicana
Purshia tridentata
Rubus strigosus
Artemisia tridentata
Chrysothamnus nauseosus albicaulis

NORTH-FACING SLOPE

Populus tremuloides
Prunus melanocarpa
Sorbus scopulina
Juniperus scopulorum
Pinus flexilis
Pseudotsuga mucronata
Ceanothus velutinus
Pachystima Myrsinites
Physocarpus malvaceus
Rubus parviflorus
Amelanchier alnifolia
Acer grandidentatum
Quercus Gambellii
Acer Negundo
Sambucus glauca
Artemisia tridentata
Purshia tridentata

BANKS OF STREAM

Salix Fendleriana
Salix amygdaloides
Acer glabrum tripartitum
Betula fontinalis utahensis
Alnus tenuifolia
Cornus stolonifera
Prunus melanocarpa

VEGETATION OF CITY CREEK CANYON—*Continued*

BANKS OF STREAM	NORTH-FACING SLOPE
Rubus parviflorus	Chrysothamnus nauseosus
Crataegus rivularis	Gutierrezia Sarothrae
Sambucus glauca	Agropyron spicatum*
Rosa Woodsii	Bouteloua gracilis*
Rosa Nutkana	Koeleria cristata*
Rhus Rydbergii	
Salix fluviatilis	
Acer grandidentatum	
Acer Negundo	
Populus angustifolia	
Populus tremuloides	
Pinus flexilis	
Picea pungens	
Abies concolor	

* These grasses are also common in all of the foothills of the valley.

An attempt was made to determine the succession in the vegetation from the valley at an altitude of 4450 feet to the canyon head at an altitude of 7800 feet. The results secured were not very positive, except that the south-facing slope being more xerophytic, the herbaceous and grass vegetation of the foothills extends farther up into the canyon on the south than it does on the north face, hence the variety in plant forms is greater on the north face, until the spruce forest is reached where conditions are similar on both faces.

Near the head of City Creek Canyon are two small lakes that help to feed the stream that flows to the city and valley below. In early April and May these lakes are fairly large; fig. 5 shows one of these lakes in April while the water was still high. This figure also shows the contrast between the vegetation of the south-facing slope with its sprinkling of conifers, and that on the north-facing slope with its denser stand of conifers. During the warmer months of the summer these lakes become almost dry, and in very hot and rainless seasons they are completely so. As the water recedes, willows and herbs come in to occupy the land. *Salix Fendleriana* and *S. lutea* seem to be the dominating willows, while *Mentha spicata, M. canadensis, Urtica Breweri,* and *Mimulus Langsdorfii* are the dominant herbs. Fig. 6 shows the lake taken the same year, but in September. If it were not for the fact that the surrounding mountains are the

same it would be difficult to believe that this is the same lake as shown in fig. 5. In fig. 6 the vegetational growth appears to be rather dense; this is because some of the herbs have grown to be almost as tall as the willows. The woody growth is really not very thick, the lake bed being covered mainly by herbs and reeds.

The reasons for the disappearance of the water here are probably two: (1) the evaporation in this region is rather great, as is shown in the notes on climatic conditions which follow this discus-

FIG. 5.—Lake at head of City Creek Canyon, April, 1923; wooded side is north face of canyon; photograph by SEVILLE FLOWERS.

sion; and (2) since the substratum is mainly of limestone it may be supposed that the seepage is considerable. This idea is further supported by the fact that lower in the canyon, underground streams come to the surface as large flowing springs.

EMIGRATION CANYON

The other unglaciated V-shaped canyon, Emigration Canyon, has its head in the same mountains of Cretaceous conglomerate rock as does City Creek Canyon. It differs from the latter, however, in that its direction is south by west, and there are scattered along the ridges outcroppings of Triassic red sandstone. The more southern direction exposes the slopes of both sides of the canyon to about the

same amount of sunlight, consequently there is shown in the vegetation on each side practically the same degree of xeromorphism. *Populus tremuloides, Abies concolor, Pseudotsuga mucronata,* and *Picea pungens,* however, come in at a somewhat lower altitude on the southeast-facing slope than on the southwest-facing slope. Other conditions seeming to be equal, this would probably indicate that the afternoon sunlight is somewhat more desiccating than the morning sun.

FIG. 6.—Same lake as in fig. 5, taken in September, 1923; photograph by SEVILLE FLOWERS.

The lower foothills and sides of the canyon near its mouth from an altitude of about 5000 to 5800 feet are covered with *Artemisia tridentata.* Below that altitude and down into the valley are grasses and herbs typical of the burned-over areas of the region.

On all the higher ridges of the canyon at an altitude of 7800 feet are to be found *Cercocarpus ledifolius* and *C. intricatus.* Below the *Cercocarpus* ridges, extending down the mountain sides into the canyon, is a wide band of *Ceanothus velutinus,* which merges into *Juniperus scopulorum* and *Quercus Gambellii.*

The next zone is a mixture of *Acer grandidentatum, Cornus stolonifera, Sorbus scopulina, Prunus melanocarpa, Amelanchier alnifolia,* and occasional *Pseudotsuga mucronata* and *Abies concolor.* This mixed vegetational zone extends down to the stream in the bottom

of the canyon, where it merges into the typical stream bank vegetation similar to that found in City Creek Canyon.

In the tributary gorges on either side of the canyon are found stands of *Populus tremuloides*, *Abies concolor*, *Pseudotsuga mucronata*, and *Picea pungens*, with a mesophytic undergrowth. The type of undergrowth found here consists of such plants as *Thalictrum Fendleri*, *Actaea arguta*, *Aquilegia flavescens*, *Claytonia lanceolata*, *Stellaria longipes*, *Pyrola secunda*, *Mertensia longifolia*, *Hydrophyllum capitatum*, *Arnica cordifolia*, *Erythronium grandiflorum parviflorum*, *Disporum trachycarpum*, *Smilacina amplexicaulis*, *S. sessilifolia*, *Pteridium aquilinum*, etc.

Glaciated canyons

The broad, open, basin-like heads, the U-shaped valley sections, and the tributary hanging valleys with their lakes are evidence of the work of the Pleistocene glaciers in the Big Cottonwood and Little Cottonwood canyons.

Little Cottonwood Canyon

This, the smaller of the two canyons studied, is a beautifully U-shaped canyon. It is 12 miles long and contained the largest glacier of the region. In some places the striae on the rocks indicate that the ice was over 1000 feet thick, and the morainal deposits show that the glacier extended down into Salt Lake Valley below the mouth of the canyon (1). The main stream bed has a general westward direction, but turns at the mouth of the canyon toward the northwest.

The chief regions of study were the main catchment basin at the head of the canyon and the region between the smooth granitic walls and the canyon mouth. There are a number of tributary valleys which have interesting formations, but no attempt was made to study them.

The evident geologic formations and their respective plant coverings from the mouth of the canyon to the head appear in the following order. Near the mouth is a collection of drift material made up almost entirely of granitic and Archean rock. The vegetation is composed of the xerophytes typical of the foothills in this region, such as the *Quercus-Rhus* and the *Artemisia-Chrysothamnus* associa-

tions, and the grass-herb association leading into the valley. Passing on up the canyon the white granitic rock becomes dominant, and for six or seven miles upstream forms its very smooth and steep walls. Here the slopes are too steep to allow any but crevice vegetation to grow, and are so smooth and precipitous as to be inaccessible for close study. In the nearer crevices the tree forms, such as *Pseudotsuga mucronata* and *Pinus flexilis*, and some of the shrubs such as *Rubus strigosus gracillipes* and *Ribes cereum*, which are typical of rock crevice vegetation in this region, could be recognized. As the granite diminishes, the Paleozoic sedimentary rocks become more abundant. The main catchment basin is almost entirely of sedimentary rock. The rocks of the slopes of this basin show the erosive effect of ice to an astounding degree. ATWOOD states:

> Every conceivable thing that the debris-laden ice might do in passing over a rock is illustrated: Chattermarks, polished surfaces, deep groves . . . and at one place six sets of striae indicating as many directions of ice-movement on a single surface.

The only lake in this main cirque, Mountain Lake, locally named Lake Minnie, is on the north-facing slope in a rock basin of red quartzite at an altitude of 9850 feet. The geologic map (fig. 7) shows the position of all the glacial lakes studied, of which Mountain Lake is one. Fig. 8 shows the setting and the type of vegetation which surrounds this lake. The water is not more than 8 or 9 feet deep and contains no visible form of plant life. There is also lacking a shore vegetation. Scattered here and there about the lake, as elsewhere on the north-facing slope, are clumps of small trees such as *Juniperus communis* and *Pseudotsuga mucronata*, and the shrubs *Ribes lentum*, *Ribes viscosissimum*, and *Jamesia americana*. Just above the lake is a rock mountain with a talus slope of shale. These rocks have no covering of vegetation, due probably to the fact that they are normally covered by snowdrifts the entire year, and the plants have not had a chance to get up so high in one dry season. Fig. 9 shows the rock formation just below Mountain Lake. Here the rocks are very smooth, and plants such as *Selaginella rupestris*, *S. densa*, and *Phlox canescens* are abundant. The trees are mainly *Pinus flexilis*, *Pseudotsuga mucronata*, and *Juniperus communis*, and the shrub *Ribes lentum* is fairly prevalent.

The south-facing slope of the cirque does not have such wide expanses of smooth rock. The slopes are more eroded and scarred by shallow gullies. The vegetation is scattered, and in patches,

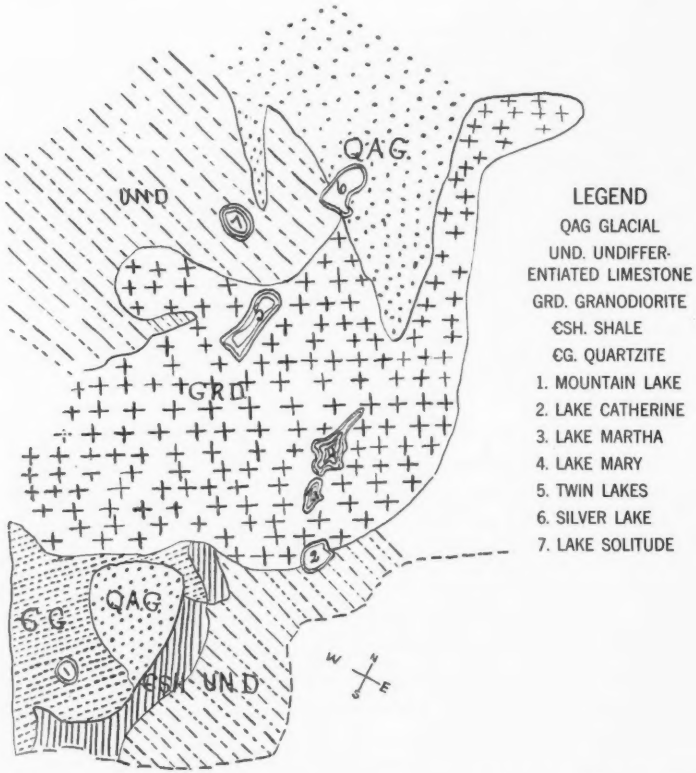


FIG. 7.—Geologic map of the Cottonwood Divide, adapted from U.S. Geologic maps in *The ore deposits of Utah* by BUTLER, LAUGHLIN, and others. Professional Paper III of U.S. Geol. Survey. 1920.

in which are found *Pinus flexilis*, *Pseudotsuga mucronata*, and *Juniperus communis*. The shrubs are *Ribes lentum* and *R. viscosissimum*. The only herbaceous plants found here are *Frasera speciosa*, *Lupinus floribundus*, and in some of the shaded rock crevices *Primula*

FIG. 8.—Mountain Lake, Little Cottonwood Canyon

FIG. 9.—Glaciated rocks below Mountain Lake, Little Cottonwood Canyon

Parryi and *Woodsia oregana*. In crevices exposed to the sun *Pellaea densa* and *P. Wrightiana* are found. The scantiness in shrubs and herbaceous vegetation is due to the work of 25,000 head of sheep which were allowed to browse here for about a week. The plants named were those left, seemingly unpalatable to the sheep. They had eaten all spineless shrubs; the willows were stripped of all foliage, and in some instances were cropped close to the ground. Most of the spaces between the clumps of evergreens were entirely

FIG. 10.—Main catchment basin in Little Cottonwood Canyon, showing effects of over-cutting and over-grazing.

bare of vegetation. This is a most deplorable condition, since it leaves the very thin layer of soil exposed to all eroding factors such as the strong westerly winds and the rainfall which is usually very heavy. This in turn naturally results in very rapid run-off, perhaps of almost "cloudburst" proportions, causing great damage lower down the canyon. These factors have already transported much of the soil elsewhere, leaving only bare rock surfaces on which it is most difficult for any plant to live. There are some lichens, but they are not very abundant.

In the bottom of the cirque conditions are not much better, although there are several small springs which aid vegetation to become more quickly reestablished. Here were found large areas of

pure stands of *Rudbeckia occidentalis*, an indication that this region has been overgrazed before. Another regrettable condition is illustrated in fig. 10. In pioneering days there was a great need for lumber, and since the timberlands in this region are high up and scattered here and there among the mountains, the most accessible trees were used. The trees in this basin apparently afforded good lumber material, and the entire stand, which was somewhat extensive and of rather large trees, was completely destroyed. It will be many generations before this area is reforested with a similar stand.

Big Cottonwood Canyon

The ridge which forms the south-facing slopes in the main basin of Little Cottonwood Canyon also forms the north-facing slopes of the main basin of Big Cottonwood Canyon. As the name implies, this canyon is the larger of the two. It also contained Pleistocene glaciers, but they were not as large as the glaciers in the Little Cottonwood, and did not extend the full length of the canyon. It is broader, longer, and has much more tributary country than has Little Cottonwood Canyon, and consequently offers a much larger opportunity for ecological study.

The main catchment basin is a broad open valley at the head of the canyon, in which is located the mountain resort of "Brighton" or "Silver Lake." Summer homes are dotted along the surrounding slopes. Tributary to the main basin are six hanging valleys, each containing rock basin lakes. The streams that flow from these lakes into the big basin join the stream from Silver Lake, the only lake in the main basin, and together they make up Big Cottonwood Creek. This creek flows northwestward until, just before it leaves the cirque, it assumes a general westward direction, which it holds throughout its course in the comparatively narrow and rugged lower canyon.

The dominant geologic formations at the head of the canyon will be mentioned in the discussion of the different portions studied. These formations are shown in fig. 7 (3).

The highest peak in the Cottonwood divide, Mount Wolverine, a steep mountain 10,650 feet high in the Granodiorite formation, is at the head of Big Cottonwood Canyon. The north-facing slope of this mountain has very little vegetation. It is too steep to per-

mit of ascent, and consists mainly of bare, rugged rock ledges on which are to be found a few lichens. On the east and west ridges leading up to the mountain peak and on the less steep south face is to be found a typical subalpine vegetation. The trees have assumed the stunted growth forms of wind timber, the shrubs are reduced in size, and the herbaceous plants are the typical mat-formers of cold regions. The trees found just below the mountain peak are *Pinus flexilis* and *Abies concolor*. The shrubs are *Ribes saximontanum* and *Arctostaphylos Uva-ursi*. This is the only place where the latter shrub was found in the entire region studied. The matted herbaceous plants are *Phlox canescens* and *Sedum integrifolium*. About 300 feet lower on the mountain side were the herbaceous plants usually found in the vicinity of snowbanks and in damp places, such as *Primula Parryi* and *Aquilegia flavescens*. In years of normal precipitation there are usually large snow banks which remain on the ground until late in August, but 1924 being an unusually dry and hot year, the snow had disappeared by mid-July.

Still lower on the mountain side, leading down into the cirque which contains Lake Catharine, the highest glacial lake of the region, at an altitude of 9850 feet are found such plants as *Macaranthera viscosa*, *Castilleja* sp., *Lupinus* sp., *Orthocarpus Tolmiei*, and *Veratrum speciosum*, which occurs in large stands near the southeast end of the lake; at the spring and along the stream feeding the lake are found *Parnassia fimbriata* and *Geranium Richardsonii*. The dominant shrubs leading down the northeast face of the mountain to the shore of Lake Catharine are *Pachystima Myrsinites*, *Ribes lentum*, *Sambucus microbotrys*, *Dasiophora fruticosa* (very abundant), and *Artemisia aromatica*. The trees here are *Pseudotsuga mucronata* and *Abies concolor*. Lake Catharine lies on two kinds of substratum (fig. 7). The southeastern half, on which this vegetation is found, is of undifferentiated limestone, and has accumulated a good layer of soil; while the northwestern half is on the Granodiorite formation and consists mainly of bare rock. Fig. 11 shows the type of vegetation found on the north side of the lake. With the exception of a few scrubby trees and woody plants which found a crevice in which to anchor, the rocks are bare. Fig. 11 also shows the paths

of drainage and snowslides into the lake, which are two of the causes for certain areas being devoid of vegetation. The only plant life visible in the lake consists of a few forms of algae.

Passing down over the northwest ridge of the Lake Catharine cirque, conditions become more mesophytic and more favorable to

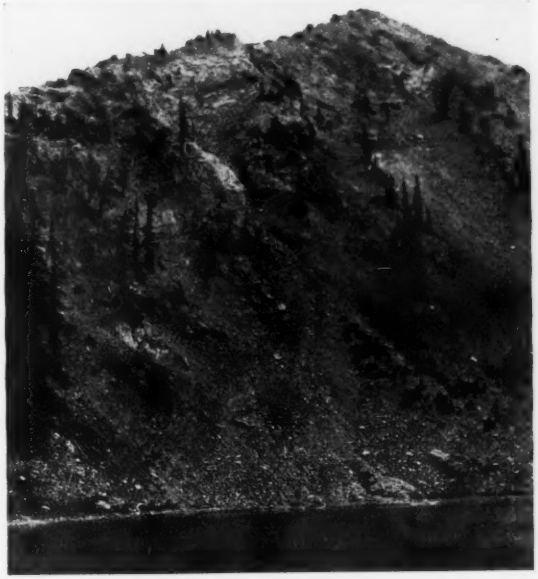


FIG. 11.—Lake Catharine in Big Cottonwood Canyon, showing course of snow slides.

plant life. The trees are in a more sheltered position and hence can obtain a more normal growth. Here are to be found such trees as *Pseudotsuga mucronata*, *Picea Engelmanii*, *Abies concolor*, and *Juniperus communis*. The shrubs are scattered in their distribution, and such forms as *Ribes lentum*, *R. coloradense*, *Sambucus microbotrys*, and *Sorbus scopulina* are found here. The rocks are kept moist by seepage water, and growing among them are the herbaceous plants *Primula Parryi*, *Aquilegia flavescens*, *Ranunculus glaberrimus*, *Saxifraga arguta*, and *Asplenium viride*.

This northwest ridge descends into a lower glacial cirque containing Lake Martha. This cirque, which is entirely in the Granodiorite formation, is 200 feet lower than Lake Catharine, and is surrounded on the east, south, and west by comparatively high and close mountains which serve as very good wind breaks. The slopes of the surrounding mountains are too steep to allow of much accumulation of soil, so that mainly a crevice vegetation is found here, with trees growing taller than those higher and more exposed. The character of the substratum of the shore and lake bottom is very different from the rocky substratum of Lake Catharine. Here there is more of an accumulation of soil, and the bottom of the lake is covered by a layer of soft mud and humus which appears to be several feet thick. The vegetational zone around Lake Martha is 15–20 feet wide, and consists of the grasses *Calamagrostis canadensis acuminatum*, *Sitanion rigidum*, and *Hordeum jubatum*, and reeds as an undergrowth to the willows which are here dominant plants. *Isoetes* with *Sparganium* grows out some distance into the water. One interesting feature about the line of willow growth is that one cannot make his way among the willows on account of the numerous *Abies concolor* seedlings which are coming in under the protection of their shade. These conifers are almost as tall as the willows, but yet not large enough to be noticed until one tries to pass through them. There is an interesting little rocky island in the lake, on which are growing *Pseudotsuga mucronata* and *Ribes lentum*. Fig. 12 shows this lake with its island, shore vegetation, and the northeast-facing slopes which are only scantily clothed with vegetation.

Just over the north rim of the Lake Martha cirque and about 100 feet lower in altitude is another glacial basin, in which is found Lake Mary. This basin at one time contained two lakes, but a dam was built across the northeast rim of the basin, making it into a reservoir for the water supply of Salt Lake City, thus raising the water and making the two lakes into one. The raising of the water caused the scanty shore vegetation to be destroyed. Now there is surrounding the basin a rim of bare, smooth glaciated rock, whose crevices hold mainly tree forms such as *Pseudotsuga mucronata*, *Picea Engelmannii*, and *Abies concolor*. Some *Juniperus communis* and *Pachystima Myrsinites* occur, with a few herbaceous plants grow-

ing here and there. The character of this lake basin and the type of vegetation which surrounds it are illustrated in fig. 13. On the west of Lake Mary is a steep rugged ridge, which separates it from the glacial basin containing the Twin Lakes. This ridge is made up of smooth glaciated bowlders which are very difficult to climb. In order to reach this third tributary cirque the trip must be made

FIG. 12.—Lake Martha with island, Lake Mary in distance, and glaciated mountain side, Big Cottonwood Canyon.

via the main basin, therefore, but no discussion of the main basin will be made until after the tributaries have been discussed.

The Twin Lake basin, like Lake Mary, has been utilized by man for a water reservoir. This basin is the largest of the tributary basins studied, and the lakes are so deep that bottom has never been sounded. The shore vegetation here, as around Lake Mary, has been greatly modified. The only herbaceous flora left near the lake is that which follows the courses of the streams coming from the springs in a small cirque just southeast of the lakes. Along these streams at an altitude of 9500 feet is a hydro-mesophytic vegetation. Here were collected a large number of mosses which will be treated

in a subsequent paper. This region is well covered by willows, a rich undergrowth of grasses, and such plants as *Mimulus Langsdorfii*, *Parnassia fimbriata*, and *Pyrola uliginosa*.

On the northwest side of the lake is a rocky ridge along the top of which *Pinus flexilis* is dominant, as it is on most of the rocky ridges within this region. Fig. 14 shows the characteristic habitat

FIG. 13.—Crevice vegetation around Lake Mary, Big Cottonwood Canyon

and growth of *Symphoricarpus porophilus*, *Lonicera utahensis*, *Dasiophora fruticosa* and the two *Ribes* species so prevalent in this region. The herbaceous plants here are *Aquilegia flavescens*, *Lappula floribunda*, *Castilleja sulphurea*, *C. lancifolia*, *Castilleja* sp., *Lupinus* sp., *Linum Kingii*, *Orthocarpus Tolmiei*, *Phlox caespitosa*, and *Mertensia ciliata*.

The west ridge drops down into a hanging valley which contains the fourth lake studied. This is Lake Solitude, so called because it is the farthest away from the main cirque and the other lakes. This

lake has almost disappeared, as it is being gradually filled by plants and humus. Fig. 7 shows it to be on a substratum of undifferentiated limestone, which has eroded comparatively easily and formed a soil suitable to plant growth. Excepting the main catchment basin, this little cirque holding Lake Solitude is the most densely vegetated of all the glacial cirques studied. The willows, aspens, and conifers

FIG. 14.—View of Twin Lakes, showing rock talus and depressions where vegetation has gained a foothold.

come to the water's edge. On all the surrounding slopes there is a scattering of *Populus tremuloides*, with *Picea Engelmannii*, *Pseudotsuga mucronata*, and *Abies concolor* appearing here and there. On the rocky ridges of the slope, as elsewhere, *Pinus flexilis* still persists. The mountain just east of the lake has on its north-facing slope a very good stand of the conifers typical of the montane forest, with a very mesophytic undergrowth. The spruce-fir forest extends along the slopes from Lake Solitude into the main cirque, where it forms the dominating type of vegetation. Occurring with the other conifers here is *Picea pungens*.

As shown in fig. 7, the main basin has a substratum of glacial alluvium, which is fertile and in undisturbed places is well covered by a xero-mesophytic vegetation. The floor of this basin has an altitude of 8750 feet, which makes the growing season limited to about three months' duration. The main shrubs found here are *Salix Fendleriana*, *S. cordata*, *S. Scouleriana*, *Lonicera involucrata*, *L. utahensis*, *Sambucus microbotrys*, *S. glauca*, *Sorbus scopulina*, *Ribes saxosum*, *R. lentum*, *Rubus strigosus*, *Bossekia parviflora*, *Physocarpus malvaceus*, *Rosa chrysocarpa*, *R. Nutkana*, *R. Fendleri*, and *R. Woodsii*.

The herbaceous undergrowth is a particularly beautiful one because of the luxuriant growth of the individual plants. *Mertensia longistylis*, *Geranium Richardsonii*, *G. Fremontii*, *Potentilla glaucophylla*, *Castilleja lauta*, *Aconitum ramosum*, *Delphinium reticulatum*, *Pedicularis racemosa*, *Aquilegia coerulea*, *Ranunculus maximus*, and *Lappula floribunda* all grow to be three to four feet high, especially in the moister places such as near the streams or around the numerous springs which flow into this basin. As in most mountain resorts, however, this flora is disappearing at a deplorable rate due to the unthinking depredations of the "nature lovers." Overgrazed patches are springing up into groups of *Veratrum speciosum* and *Frasera speciosa*, and *Rudbeckia occidentalis* is becoming much too prevalent.

Where the trees are thickest and the ground is shaded and moist there are many interesting underplants, such as orchids, and species of *Pyrola*, *P. uliginosa*, *P. secunda*, *P. chlorantha*, *Limnorchis*, *Mitella pentandra*, and *Tellima parviflora*. There are only a few kinds of ferns in this region: *Woodsia* and *Pellaea* that have been named as growing in the rock crevices, *Pteridium aquilinum*, and *Filix fragilis*, which is found in only one place in the main canyon. It was formerly found in several places, but tree cutting and changing water courses have caused it nearly to disappear.

The mesophytic vegetation continues down the canyon along the stream course for a distance of about four or five miles, when conditions gradually change. Taking the place of *Pinus flexilis* along the mountain ridges is *Cercocarpus*, and lower on the mountain slopes are to be found *Ceanothus velutinus* and *Quercus Gambellii*. *Pseudotsuga mucronata* is the most persistent conifer, and extends down the

canyon farther than any of the other evergreens. At about 7500 feet altitude the stream vegetation which has been named as characteristic of the other canyons becomes the dominating feature, and continues down into Salt Lake Valley.

Pinus scopulorum is reported as occurring naturally on only one site, which is on the south-facing slope at an altitude of about 6400 feet (**8**). I did not see this natural stand of yellow pine, but I did see scattered clumps of seedlings planted by the United States Forestry Service, which has a station in Big Cottonwood Canyon at an altitude of 7400 feet. These pines have therefore not been listed in the native vegetation. The isolated groups of native *Pinus scopulorum* make an interesting problem for future investigation. There are also a few yellow pines occurring in Parley's Canyon, which is a few miles north of Big Cottonwood Canyon. It has been reported that these trees of *P. scopulorum* are the farthest north until those of Idaho and Wyoming are reached.

Climatic conditions

PRECIPITATION.—The district covered by this survey is in the semi-arid section of the United States, but the wide variation in altitude results in widely differing amounts of precipitation in different parts of the area studied. At the level of Salt Lake City, 4408 feet, the average precipitation, most of which is rainfall, is about 16 inches, while at the head of Big Cottonwood Canyon at 8700 feet it is about 43 inches, of which a good deal is snowfall. ALTER'S (**2**) study of the relation between precipitation and altitude shows that on the western slopes of the Wasatch Mountains there is an increase of about 4 inches per year per 1000 feet.

TEMPERATURE.—Very wide variations of temperature are found in the area herein considered. These variations are not only seasonal but diurnal. Even at the level of Salt Lake City the annual temperatures vary from a summer maximum of about 107° F. to winter temperatures of about zero. Very much lower winter temperatures are of course found at the higher altitudes, and diurnal variations are of course greater there also.

The annual mean temperature taken from 45 years' record at Salt Lake City is 51.6° F., while the mean average from May to

October as recorded at the Big Cottonwood Nursery (7450 feet in altitude) is 51.9° F. The mean average for the same months in Salt Lake City is 65.2° F. Air temperatures decrease quite uniformly with increase in altitude, and it is thought that the usual relation holds in a general way here; that is, that the temperature gradient is about 3.5° F. for each 1000 feet (2). Table I gives the mean temperatures by months in degrees F. for Salt Lake City and Big Cottonwood Nursery, Utah (2).

TABLE I

MEAN TEMPERATURES

	JAN.	FEB.	MAR.	APR.	MAY	JUNE	JULY	AUG.	SEPT.	OCT.	NOV.	DEC.
Salt Lake City, altitude 4408	29.2	33.4	41.8	49.9	57.4	67.1	75.6	74.6	64.4	52.5	40.9	32.1
Big Cottonwood Nursery, altitude 7450	....	....	....	....	42.5	55.2	62.4	60.0	51.8	39.5	....	....

From the preceding data it can be seen that in Salt Lake City there are usually four months of the year (November, December, January, and February) that are below 40° F. and hence unsuitable to plant growth; while at an altitude of 7450 feet there are six months with temperatures too low to permit vegetation. At the highest altitude reached in this investigation the growing season probably does not exceed three months.

EVAPORATION.—Evaporation is very rapid because of the high summer temperatures and low humidity. The average annual evaporation on the shores of Great Salt Lake is about 80 inches, consequently in this region we get plants of desert types. In the canyons evaporation is lessened on account of the decrease in temperature as compared with the evaporation in the valley. Also, greater summer precipitation in the canyons tends to offset evaporative action, so that at an elevation of 7500 feet the net evaporation from June to September averages about 24 inches. In the canyon bottoms and on the lower slopes, the effects of evaporation are offset by the water supply from the springs and streams, a condition which is not attained either at a higher elevation or in the valley. The effects of evaporation, therefore, are among the more important factors affecting the type of summer flora found in the different parts of the region studied.

Summary

1. SALT LAKE VALLEY (extreme eastern portion of Great Basin).—This is occupied by two different types of vegetational composition, due to soil conditions. The soil on the west side of the Jordan River being of alkaline nature, is covered by a sparse growth of alkali-tolerant plants. The soil on the east of the Jordan River is higher, well drained and fertile, and is mostly cultivated.

2. UNGLACIATED CANYONS.—These show a succession from the grass covered foothills, through sage brush and oak chaparral to an aspen-spruce forest at their heads. The City Creek Canyon which has a west-by-south direction is xerophytic for a longer distance up the canyon on the south-facing slopes. Emigration Canyon, which has a southwest direction, shows practically the same kind of vegetation on both slopes of the canyon; the east-facing slope may be a little more mesophytic than the west, since the aspens come in somewhat lower on the east face.

3. GLACIATED CANYONS.—Where not disturbed by fire, overgrazing, and overcutting, these show the same vegetational successions as the unglaciated canyons. These canyons are more rugged, however, are deeper, and go to higher altitudes, developing on the higher north-facing slopes a good stand of the spruce-fir montane forest, which gives way at about 10,000 feet to a subalpine flora. The area here reaches just a few feet above timber line.

Conclusions

The differences that occur in the vegetational cover of Salt Lake Valley and the lower adjacent canyons are due almost entirely to edaphic factors. In the valley the differentiation is caused mainly by the accumulation of alkali salts in the land west of the Jordan River. On the fertile or salt-free land east of the river the limiting factor seems to be water, for where water is supplied the canyon vegetation extends into the valley. Also the fact that with irrigation such mesophytic crops as peaches and apricots grow successfully would indicate that water might be the limiting factor.

The changes which occur in the character of the vegetation as one ascends the canyons in all probability are due to the gradual changes in climate and soil conditions. The high ridges are mostly rock and intercept the strong westerly winds of this region, so that

one would expect only the wind forms and the xerophytic type of vegetation which are found there. The observations of other ecologists were confirmed to the effect that the north-facing slopes retain more moisture than do the south-facing slopes, and hence show a greater development of the mesophytic type of vegetation.

The native vegetation of the entire region has been greatly modified by the activities of civilization: for instance, great areas have been subjected to over-grazing by cattle and sheep; the scant timber supply has had to be used for man's immediate need of housing and fuel; much of the land has been put under cultivation, and many of the streams and lakes have been utilized for domestic and industrial purpose. It appears logical, therefore, to conclude that many of the factors influencing the character of the vegetation described herein are those of a biotic nature.

Notwithstanding the modifying effects of agriculture, logging operations, and grazing, however, there remains ample evidence that the native flora in the area studied is determined by the natural conditions of soil, altitude, precipitation, temperature, evaporation, and length of growing season, and varies in type and characteristics as these factors vary. This is shown by the changes in the native flora from desert forms to subalpine types, depending on location as described and listed in this study.

Grateful acknowledgment is made to Professor H. C. COWLES and Dr. G. D. FULLER for the helpful suggestions which have aided in the preparation of this paper.

SMITH COLLEGE
NORTHAMPTON, MASS.

[*Accepted for publication February 26, 1926*]

LITERATURE CITED

1. ATWOOD, W. W., Glaciation of the Uinta and Wasatch Mountains. pp. 96. Illus. and maps. 1909.
2. ALTER, J. C., September Monthly Weather Review for Utah. U.S. Dept. Agric. Weather Bur. 1919.
3. BUTLER, B. S., and LOUGHLIN, G. F., The ore deposits of Utah. Prof. Paper 111. U.S. Geol. Sur. pp. 657. Maps. 1920.

4. COULTER, J. M., and NELSON, A., Manual of Rocky Mountain flora. New York: Amer. Book Co. 1909.
5. GARRETT, A. O., Spring flowers of the Wasatch.
6. GILBERT, G. K., Lake Bonneville. U.S. Geol. Sur. Mon. 1. XX. pp. 438. 1890.
7. KEYES, C. R., Orographic origin of ancient Bonneville of Utah. Geol. Soc. Amer. Bull. **28**: no. 2. pp. 351–374. 1907.
8. KORSTIAN, C. F., Density of cell sap in relation to environmental conditions in the Wasatch Mountains. Jour. Agric. Res. **28**:845–907. 1924.
9. LEWIS, R. S., and VARLEY, T., The mineral industry of Utah. Bull. 12. Univ. Utah. **10**: pp. 199. 1919.
10. RYDBERG, P. A., Flora of the Rocky Mountains and adjacent plains. New York. 1917.
11. The soils of Salt Lake Valley, Utah. Dept. Agric. Div. Soils Cir. 4. 1899.

SEASONAL DEVELOPMENT OF GROWTH LAYERS IN FRAXINUS CAMPESTRIS AND ACER SACCHARINUM

HERBERT C. HANSON AND BERNICE BRENKE[1]

(WITH PLATES XIX–XXI AND TWO FIGURES)

Introduction

Considerable investigation has been done on the increase in diameter of trees. The literature up to 1915 has been excellently summarized by GROSSENBACHER (7). Much work remains to be done, however, as we know little or nothing about the behavior of many species, about the behavior of trees in many regions, and the behavior of the same species in different seasons. The aims of this study were to discover when xylem formation began and ended, the rate at which new xylem cells were produced, and to compare the course of xylem formation with environmental factors, to see whether there was any correlation. The trees used were *Fraxinus campestris* Britton, forming ring-porous wood, and *Acer saccharinum* L., forming diffuse-porous wood. This study was carried on during the growing season of 1925, in the vicinity of Lincoln, Nebraska.

Methods

Trees were cut down at intervals from March 23 to October 14. The ash trees were growing in an open forest on the floodplain of Salt Creek, about 3 miles southwest of Lincoln. The soft maples grew in a grove of small trees and shrubs in rich soil on a vacant lot on the upland, about 5 miles northeast of Lincoln. The ash trees ranged from 10 to 40 years in age, the soft maples from 8 to 14 years. Small blocks about an inch long, half an inch wide, and a quarter of an inch thick, containing the outer xylem and the inner phloem, were cut from a height of one foot above the soil. Blocks were taken in duplicate from opposite sides of the trunk on each

[1] Miss BERNICE BRENKE prepared the slides and helped considerably with the drawings; the senior author did the rest of the work and assumes responsibility for all statements.

date, and were kept in a solution containing equal parts of glycerine and 95 per cent alcohol before cutting sections on a sliding microtome. The sections were cut 30–40 μ thick, immersed for a short time in Eau de Javelle to remove the protoplasmic contents of the cells, stained with safranin and Delafield's haematoxylin, and then permanently mounted. This procedure made the cell walls stand out clearly, and showed good differentiation between the lignified and cellulose walls.

Although a different tree was used on each date, the results of the study appear important enough to warrant publication, especially since very little or no work of this sort has been done on these two species, so far as the writers could determine. Investigators have shown that trees of the same species, even when growing close together, vary considerably in xylem production. The advantage in using a different tree on each date, therefore, is that the general course of development of a number of individuals is secured in place of the development of a single tree which might be abnormal in its behavior. Since fourteen determinations were made for each species during the growing season, the sections were taken closely enough together so that they serve as checks upon one another.

Development in Fraxinus campestris

MARCH 28.—The buds were only slightly swollen, no green showing (fig. 1). The bark adhered firmly to the wood. The width of the cambium was 4–6 cells, averaging about 31.5 μ. No new xylem cells had formed. The age of the tree was 33 years; diameter 4.5 inches.

APRIL 15.—The tree was in full bloom, the leaves were just beginning to expand but showed no green (fig. 2). The bark separated from the wood at the cambium very easily, leaving the exposed surface rather watery. Age 35 years; diameter 5 inches.

The width of the cambium layer was 4–6 cells, about 35 μ. The maximum width of the new xylem was 88 μ; the largest tracheary tubes were 105 μ in tangential diameter. Tracheary tubes were forming rapidly.

APRIL 20.—The leaves on the tree were about 1.2 inches long, the longest terminal growth of twigs 0.5 inch (fig. 3). The bark did not separate from the wood quite as easily as on April 15, but the

newly exposed surface was very wet and somewhat viscous. Age about 40 years; diameter 4.5 inches.

The thickness of the cambium was 5–8 cells, about 45.5 μ. The maximum width of the xylem was 189 μ; the maximum diameter of the tracheary tubes was 189×235 μ. The tracheary tubes were developing rapidly, and the walls of the larger tracheary tubes were a little thicker than those of the other cells.

APRIL 27.—The oldest pair of leaves were 5–7 inches long (including the petiole); the largest leaflets (lowest pair on a leaf) were 1×3 inches, the upper pairs were smaller, 0.5–0.7×1.5–2.0 inches. The tree appeared fairly leafy (fig. 4). Terminal growth of twigs averaged about 3.5 inches long. Age of tree about 45 years; diameter 5.2 inches.

The thickness of the cambium was 5–9 cells, about 52.5 μ. The maximum width of the xylem was 360 μ. The innermost row of tracheary tubes had reached full size (225×240 μ), and the walls of most of them were thickened (3.5–7 μ thick) and lignified like the mature tubes of the preceding year. The other large tubes, nearer the cambium, were enlarging rapidly. Often the first row and in places some of the cells in the second row of cells surrounding the lignified tracheary tubes were beginning to lignify their walls. The development of the new xylem in one-year old and 1925 twigs was about the same as at the base of the trunk, except that lignification was slightly more advanced and the ducts were much smaller and more numerous in the twigs.

MAY 4.—The lowest three pairs of leaves on the twigs were usually 5–7 inches long, with leaflets averaging about 1×3 inches in area. The increase since April 27 in leaf area had been great. Individuals varied considerably in the rate of leafing out. The fruits on this tree were about one-eighth of an inch long. The terminal growth of the twigs varied from 1 to 5 inches, and on some twigs terminal and axillary buds had formed, but on other twigs leaves were still being produced. This tree was 5.5 inches in diameter and 45 years old.

The width of the cambium was 5–9 cells, averaging about 52.5 μ. The maximum width of the xylem was 345 μ, and the inner part, about 150–225 μ wide, was partially thickened and lignified. The

first row or two of cells surrounding the inner tracheary tubes had walls about 3.5 μ thick, and the rest of the cells between the tracheary tubes had walls about 1.8 μ thick. The thickness of the walls of the tracheary tubes was similar to those of the April 27 specimen. The outer edge of the lignified region was wavy, due to the earlier thickening and lignification of the tracheary tubes followed by the

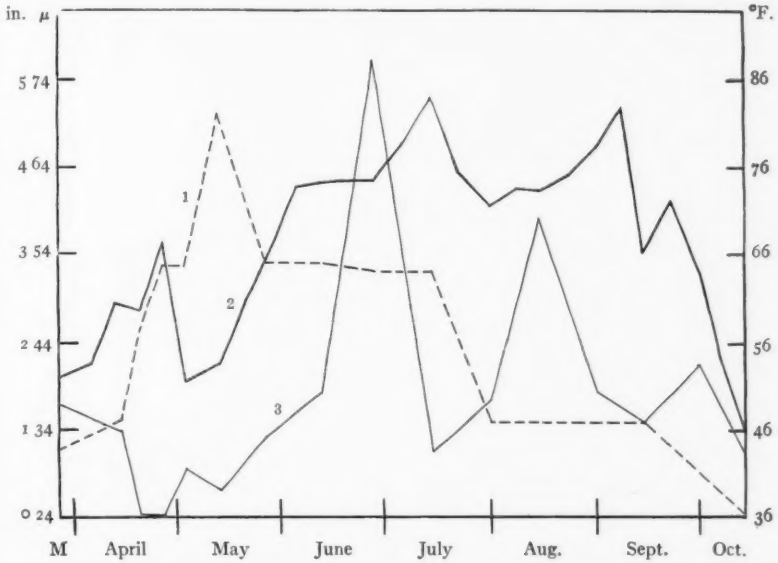


FIG. 1.—1, Width of cambium layer in *Fraxinus campestris* in microns during season of 1925; 2, mean temperature for intervals of about 7 days; 3, total precipitation for intervals between cambium measurements.

wood fibers between them. All of the large tracheary tubes (reaching a diameter of 225 μ) were fully developed, and only the outer ones (90 μ or more) outside of the 1924 xylem were unlignified. Many smaller tubes, 75 μ or less in diameter, were being formed outside of the large ones, and these showed no lignification.

MAY 14.—The lowest two pairs of leaves on the twigs were usually 6–7 inches long, the rest 3–5 inches (fig. 5). The leaflets on the lower two pairs of leaves were about 1×3 inches in area. The

tree appeared quite leafy, but some of the leaves were not fully grown yet, and different individuals still showed considerable variation in leaf development. The terminal growth of the twigs varied from 1 to 4.5 inches. The diameter of the tree was about 5 inches; age 14 years.

The width of the cambium was 7–9 cells, about 70 μ. The maximum width of the xylem was 750 μ, the inner lignified part being 450–750 μ wide. All of the large ducts (2 or 3 rows) were fully thickened and lignified, reaching radial diameters of 300 μ. The cells immediately adjacent to these ducts had walls about 3.5 μ thick, but the other cells between the ducts in the lignified part had walls 1.8 μ or less thick. The activity of the cambium was great at this time.

MAY 27.—The lowest three or four pairs of leaves on the twigs were 6–8 inches long (including the petiole). The leaflets averaged about 1.2×3 inches in area. Many young leaves and stem tips were brown or black from the effects of frost. The terminal growth of the twigs ranged up to 14 inches. The tree appeared quite leafy. The diameter was about 4.5 inches; age 14 years.

The width of the cambium was 7–9 cells, about 53 μ. The maximum width of the xylem was 645 μ, the inner part (330–570 μ wide) partially lignified. There were 1.5–2 rows of large ducts, the largest 225 μ in diameter, all fully thickened and lignified except an occasional one farther out. The cells between the tracheary tubes, except for the row or two surrounding the tubes, were usually about 1.8 μ thick. Many small tracheary tubes were being formed, and the activity of the cambium was still great.

JUNE 13.—The leaves appeared fully grown, the lower pairs averaging about 8 inches long with leaflets about 1.2×4 inches (fig. 6). The terminal pairs were smaller and no new leaves were being formed. The tree was very leafy. The terminal growth of the twigs was 2–8 inches. The twigs were stiffer than on May 27, brown streaks and blotches were developing in the bark, and the lenticels were white and prominent. The diameter was 5.2 inches; age 29 years.

The thickness of the cambium was 7–9 cells, about 53 μ. The maximum width of the 1925 xylem was 720 μ, the partially lignified

part 450–645 μ. There were 2 or 3 rows of large ducts, the largest 225 μ in diameter, all of which had fully thickened and lignified walls. Many of the smaller ducts (about 60 μ in diameter) were also fully thickened and lignified (walls 5–7 μ thick), and partially lignified ducts were found only 2–4 cells away from the cambium. The walls of the cells between the large ducts averaged about 3.5 μ thick, and these thick walled cells extended out, forming a row or two around many of the small ducts. The walls of the other cells between the ducts were about 1.8 μ thick. The activity of the cambium appears to have become retarded, but new cells, including a number of small ducts, were still being formed. The zone of unthickened and unlignified cells was much narrower than before, so that lignification had been going on rapidly.

JUNE 28.—Due perhaps to the rainy weather in the preceding two weeks, renewed growth from terminal buds had produced clusters of up to 5 or 6 small, tender leaves on new stems (fig. 7). The new terminal growth was 1–2 inches long. The dry weather before June 13 may have caused premature development of the terminal buds. The leaves below these clusters of new leaves were fully developed, as indicated by their stiffness, color, and size. If the dry weather had continued it is likely that no new leaves or terminal growth would have been produced. The 1925 portions of the twigs were fairly stiff, but could be bent beyond 90° without breaking. The brown spots in the bark of the 1925 twigs were larger than on June 13, the yellow or brownish tinge of the entire twigs was more pronounced, and the conspicuous lenticels were pale brown. The diameter of the trunk was 4.5 inches; age 20 years.

The cambium was 7–9 cells wide, about 52 μ. The maximum width of the xylem was 1710 μ. The lignified part of the xylem was 1560 μ wide, 70 per cent (forming an inner zone) being fully lignified, with walls 3.5–7 μ thick. The rest of the lignified cells between the ducts had walls about 1.8 μ thick. There were 2 or 3 rows of large ducts, and the small ducts were fully lignified to within 150 μ of the cambium. The activity of the cambium had lessened considerably, but new ducts and other cells were still being formed. Lignification had been progressing very rapidly, the unthickened and unlignified zone averaging only about 150 μ in width.

JULY 15.—Leaves were fully developed and no new ones were forming (fig. 8). The terminal buds for 1926 were about 0.5 inch long. The terminal growth of the twigs was as much as 11–15 inches, and elongation had ceased. The bark was greenish brown, slightly greener than the 1924 portions. The lower 3–6 inches of the 1925 growth broke with a snap rather easily instead of bending, but the upper part could be bent beyond 90° without breaking. The lenticels formed conspicuous whitish streaks up to about 0.25 inch long. The sap at the cambium was more viscous and less watery than heretofore. The diameter was 5.7 inches; age 33 years.

The cambium on the sides of the trunk which were examined was about 8 cells wide, or about 52 μ. The maximum width of the xylem on one side of the trunk was 1875 μ, of which about 1725 μ was lignified. An inner zone, 1125–1425 μ wide, was completely lignified (walls 4–7 μ thick), and the outer zone of the lignified portion, 300–600 μ wide, was considerably lignified (walls 3.5–5 μ thick). A narrow zone, only 75–150 μ wide, was unlignified. Cambial activity had lessened so that only a few new cells were being formed. On the opposite side of the trunk the cambium had apparently ceased producing new cells, and the xylem, maximum width 975 μ, was lignified to the cambium. The cells in the outer zone of the xylem, 125–140 μ wide, had walls 1.8–3 μ thick; in the next inner zone (about 115 μ wide) the walls were about 3.5 μ thick; and in the inner zone they were 4–7 μ thick. Lignification was being completed rapidly.

AUGUST 1.—No new leaves had appeared (figs. 9, 10). The terminal buds were well developed. The 1925 part of the twigs was all brownish gray, but was more pliable than the 1924 part, as most of it could be bent beyond 90° without breaking. The sap at the cambium was less watery than on July 15. The diameter was 4 inches; age 19 years.

The cambium was 6 or 7 cells wide, about 35 μ. On one side of the trunk the xylem, reaching a maximum width of 675 μ, was completely thickened and lignified to the cambium. Although the outermost xylem cells were narrow like the last ones formed during the season, an occasional new cell was developing. On the opposite side

of the trunk the formation of xylem cells had ceased and had later started anew. This was shown by the layer (about 56 μ wide) of narrow cells with thick walls inside of the cambium. This outer layer of xylem consisted of larger cells with very thin walls. The remainder of the xylem was completely lignified (walls 4–7 μ thick) except the outer portion, about 70 μ wide, which had walls that were usually 3.5 μ wide. The maximum width of the xylem on this side was 960 μ, 88 per cent of which was fully lignified.

AUGUST 15.—No new leaves had appeared (fig. 11). The terminal growth this year showed as much as 10–16 inches' elongation. The distal 4–8 inches had come from the renewed activity of the terminal bud. The 1925 part of the twigs broke with a snap when bent as far as 90°. The sap at the cambium was quite viscous. The diameter was 4.2 inches; age 10 years.

The cambium was 6 or 7 cells wide, about 35 μ. The maximum width of the xylem on one side was 3825 μ and the walls were completely thickened and lignified (3.5–7 μ thick). Occasionally a narrow cell adjacent to the cambium appeared to be still thickening its walls. On the opposite side of the trunk, where the maximum width of the xylem was over 5250 μ, the cambium was slightly more active because there was a zone of xylem, about 35 μ wide, adjacent to it with walls only slightly lignified. The rest of the xylem was completely lignified. On the whole, the formation of new xylem cells had almost ceased in this tree.

SEPTEMBER 14.—The leaves were quite hard and stiff, a few had turned brown, and brown spots were common (fig. 12). The upper 2–4 leaves on the twigs had fallen, and the terminal 0.5–1 inch of the stems was dry. The 1925 part of the twigs resembled the 1924 part in color and brittleness. The buds were deep brown. The sap at the cambium was much drier than heretofore. The diameter was 5 inches; age 11 years.

The cambium was 6 or 7 cells wide, about 35 μ. The new xylem on one side was 5250 μ wide; on the opposite side 4500 μ. It was completely lignified, and the demarcation of xylem and cambium was very sharp. Formation of new xylem cells had ceased.

OCTOBER 14.—The leaves had fallen. The bark did not separate as easily at the cambium as before, and there was considerable moisture in the outer xylem and the inner phloem. The diameter was 5.5 inches; age 36 years.

The cambium was 3–5 cells wide, about 24 μ. The xylem in this tree was only 1925 μ wide, all of which was completely lignified.

Development in Acer saccharinum

MARCH 23.—The tree was in full bloom but the leaves were not yet out. The trunk was very full of sap, the sawdust forming a pasty mixture with it. The diameter was 4.5 inches; age 10 years.

The cambium was fairly thick walled, 3 or 4 cells wide, or about 17 μ. No new xylem.

APRIL 13.—The leaves averaged about 1×1 inch, pale green or reddish in color (fig. 13). The sap was not so watery as on March 23. There was considerable variation in the rate of leafing out, some trees having no leaves yet out and some with leaves 2×2 inches in area. The diameter was 4 inches; age 8 years.

Cambium was the same as on March 23; no new xylem.

APRIL 20.—The leaves averaged about 2×2 inches, were very thin, and somewhat reddish or yellowish green (figs. 14, 15). The stems had elongated up to 0.5 inch. The bark separated from the wood at the cambium readily, leaving the exposed surface very watery and slightly viscous. Sap was not so watery as on March 23. The fruit was about full grown but green. The diameter of the tree was 3.7 inches; age 7 years.

On one side of the trunk the cambium was about 12 cells wide, or 52 μ. The maximum width of the new xylem was about 105 μ, or about 10–12 cells. The largest tracheary tubes were 32 μ in diameter. All the cell walls were very thin. Growth on this side had been going on for only a short time, and was now proceeding very rapidly. On the opposite side of the trunk the cambium was about 8 cells wide, 35 μ. Production of new xylem cells had just started, one row about 10 μ wide having been formed. No tracheary tubes could be distinguished.

APRIL 27.—The leaves averaged about 2.5×3 inches and had a good green color. The greatest elongation of the twigs was about 2

inches. The fruits were full grown and beginning to dry. The sap was very watery. The diameter was 4.5 inches; age 12 years.

The cambium was about 8 cells wide, or 32 μ. Growth had just started. Only occasionally had a new xylem cell reached full size.

At a height of 8 feet from the ground, where the trunk was 3 inches in diameter and 9 years old, the new xylem was about 52 μ wide. There was a conspicuous ring of tracheary tubes with tangential diameters up to 52 μ. The walls of all the cells were very thin, and lignification had not started. The cambium was 12–15 cells wide, about 70 μ.

At a height of 18 feet from the ground, where the main stem was 2.5 inches in diameter and 4 years old, the new xylem was 80–105 μ wide (fig. 16). There were many tracheary tubes up to 52 μ in diameter, the inner ones having slightly thicker walls than the rest of the xylem. The cambium was 12–15 cells wide, about 70 μ.

In one-year old twigs the new xylem was 70–105 μ wide, with many ducts up to 52 μ in diameter (fig. 17). The walls of most of the ducts in the inner 48 μ of the new xylem were partly thickened and lignified, about 1.7 μ thick. The cells immediately surrounding these tubes had slightly thickened walls. The cambium was about 10 cells wide, 35–70 μ.

The cross-section of the 1925 portions of the twigs resembled the cross-section of an herbaceous stem, in that the bundles were separated (fig. 18). The xylem in some of the bundles reached 175 μ in width, of which about 140 μ were partly thickened and lignified. The walls of the tracheary tubes averaged about 3.5 μ in thickness. The maximum diameter of the tracheary tubes was about 32 μ. The cambium was 7–9 cells wide, 35–52 μ.

MAY 7.—The lowest two pairs of leaves on the twigs were about 3.5×4.5 inches, the upper ones were smaller (fig. 19). The tree appeared quite leafy. There was much sap in the wood. The terminal growth varied from 0.7 to 2.5 inches in length. New buds were just beginning to appear.

The cambium on one side of the trunk was about 20–25 cells wide, about 135 μ. The maximum width of the new xylem was 390 μ, of which the walls of the inner part, 135 μ wide, were slightly thickened and lignified (walls about 1 μ thick). The tracheary tubes

in this zone had reached full size, the largest being about 75 μ in diameter. On the opposite side of the trunk the cambium was about 15 cells, or 75 μ thick. Cell division was very rapid at this time.

MAY 14.—Many of the leaves appeared mature, as they were 5 to 6 inches broad by about 4 inches long; they were much stiffer than before. New leaves were being produced. The elongation of

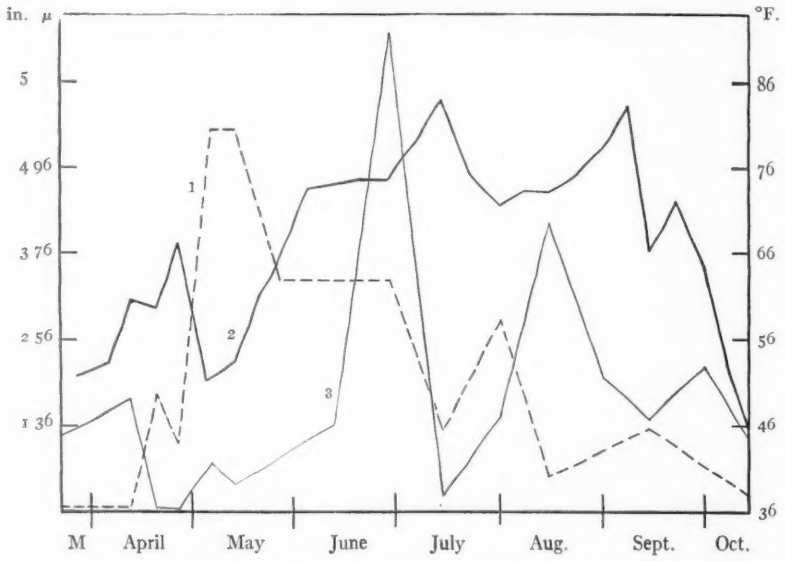


FIG. 2.—1, Width of cambium layer in *Acer saccharinum* in microns during season of 1925; 2, mean temperature; 3, total precipitation.

the terminals ranged from 1 to 3.5 inches. The diameter was about 4 inches; age 14 years.

The cambium was about 15 cells wide, or 105 μ. The new xylem was 420 μ wide. The inner part, about 300 μ wide, was partly thickened and slightly lignified. The inner half of the lignified part had walls 1.7–3.5 μ thick. The walls of the ducts were similar to those of the other xylem cells. The formation of new xylem cells was proceeding very rapidly.

MAY 27.—Most of the leaves, about 4×4–6 inches in area, were mature, as indicated by the deep green color, thickness, and firmness

of the blades (fig. 20). New leaves were being formed. Elongation of the terminals was up to 8.5 inches. The diameter of the tree was 3.5 inches; age 10 years.

The cambium was 12–15 cells wide, about 70 μ. The width of the new xylem was 990 μ. The inner part, about 825 μ wide, was partly thickened and lignified. Two zones could be distinguished in this, the inner about 522 μ wide with walls about 3.5 μ thick, and the outer about 303 μ wide with walls 1–1.5 μ thick. Cell division, thickening, and lignification were proceeding rapidly.

JUNE 13.—New leaves were still appearing, but the rate of the formation of new leaves had decreased considerably (fig. 21). The tree was very leafy. The terminal twigs had elongated up to 14 inches. The lower half of the new terminal growth had conspicuous brown lenticels, the upper half had white lenticels. The portion of the twigs with brown lenticels was much stiffer than the other part. The diameter was 4.5 inches; age 10 years.

The cambium was about 15 cells wide, or 70 μ. The xylem was 2775 μ wide, of which only a narrow zone, 180 μ wide, adjacent to the cambium was thin walled and unlignified. The innermost zone of the xylem, about 2222 μ wide, had walls 3.5 μ thick but was not mature; the outer zone, about 375 μ wide, had walls 1.2–1.7 μ thick. On the opposite side of the trunk the xylem was 2730 μ wide. Cell division was very active on this date, and lignification was proceeding rapidly.

JUNE 29.—More leaves had reached maturity (fig. 22). New leaves were still forming and some of the new terminal buds had opened, due perhaps to the moist weather of the preceding two weeks following the previous hot dry period. The twigs were stiffer than on June 13. The diameter was 4 inches; age 8 years.

The cambium was about 15 cells wide, or 70 μ. The 1925 xylem was 2640 μ wide. The thin walled and unlignified zone was about 225 μ wide. The innermost part of the xylem, about 1590 μ wide, was fully lignified, with walls 5–7 μ thick. The demarcation of this inner zone was very conspicuous. The next outer zone, about 525 μ wide, had walls 1.8–3.5 μ thick. In the outer zone of the lignified part, about 300 μ wide, the walls were only slightly thickened and lignified. In the opposite side of the trunk the xylem was 2925 μ

wide, of which the inner zone, 1700 μ wide, was fully lignified. Cell division was very active, thickening and lignification of the walls was following rapidly. About 60 per cent of the xylem formed by this date was fully lignified.

JULY 15.—New leaves were still appearing, clusters of young leaves being conspicuous at the ends of many branches (fig. 23). The elongation of the topmost terminals was up to 14 inches. Most of the upper side of the 1925 portions of the twigs had turned brown but the under side was green. Twigs were stiffer than before, but did not break readily when bent. The sap appeared more viscous than before. The diameter was 3.5 inches; age 8 years.

The cambium was 7 or 8 cells wide, about 35 μ. The 1925 xylem was 2445 μ wide. The unlignified and unthickened zone was usually not more than 16 μ wide. The innermost, mature zone of the xylem, walls 5–7 μ thick, was about 1060 μ wide. The zone outside of this one, walls 3.5–5 μ thick, was about 1155 μ wide, and the next zone, about 210 μ wide, showed tracheary tubes with walls 3.5 μ thick and the cells between with walls only slightly thickened and lignified. In the opposite side of the trunk the new xylem was 2625 μ wide, the innermost 930 μ being mature. The production of new cells had decreased considerably, and thickening and lignification were proceeding rapidly.

AUGUST 1.—The number of leaves produced on single twigs ranged up to 73, and many new leaves were still appearing (fig. 24). The terminal growth was up to 24 inches, the distal 3–6 inches having grown from the terminal bud formed this summer. There were many short shoots on the basal part of the 1925 portion of the twigs, having grown from lateral buds formed this summer. The bark was attached more firmly to the wood than before, and the sap at the cambium was much less watery. The diameter was 4.2 inches; age 8 years.

The cambium was 10–14 cells wide, about 61 μ. The new xylem was 6225 μ wide, forming three zones. The innermost zone, about 5790 μ wide, was mature with walls 3.5–7 μ thick; the next one, about 225 μ wide, had walls ranging from only slightly thickened and lignified to 3.5 μ thick, and the outermost zone, about 210 μ wide, had walls only slightly thicker than the cambium. In the opposite

side of the trunk the xylem was about 4665 μ wide, 4290 μ being mature. Cell division was still very active in this tree, and complete lignification was far advanced, about 92 per cent of the xylem being mature.

AUGUST 15.—New leaves had ceased appearing (fig. 25). The smallest leaves were about 1×1 inch in area, but all appeared mature or nearly so, as indicated by the degree of cutinization, firmness, and white undersurface of the blades. The buds for 1926 were quite prominent, about 2.5 mm. long at the tips of the branches. The elongation of the twigs was up to 15 inches. The 1925 part of the twigs could still be bent beyond 90° without breaking. The sap at the cambium was viscous. The diameter was 5 inches; age 12 years.

The cambium was about 5 cells wide, or 24 μ. The 1925 xylem was 4440 μ wide and completely lignified to the cambium. The walls of the cells bordering the cambium were 3.5–5.2 μ thick, and the cells were narrow like the last formed during the season. The other side of the trunk was similar. Cell division had ceased.

SEPTEMBER 14.—The leaves were hard, stiff, and brittle, and no new ones had appeared since August 15 (fig. 26). The 1925 portions of the twigs were deep brown. They were brittle, breaking readily when bent beyond 90°, except the distal 1–3 inches, which was still green and very pliable. The sap at the cambium was much less abundant. The diameter was 3.5 inches; age 8 years.

The cambium was about 7 cells or 35 μ. The 1925 xylem was 2580 μ thick, completely lignified except for an outer zone about 60 μ wide, which was thin walled and unlignified. In this thin walled zone new tracheary tubes were being formed as well as other xylem cells. On the opposite side of the trunk the xylem was 2015 μ wide, and the thin walled zone about 30 μ wide. In this tree cell division had ceased for the season, as indicated by the narrow, thick walled cells on the outer edge of the mature xylem, and then it had resumed again to produce the thin walled zone of larger cells bordering the cambium.

OCTOBER 15.—The leaves were still green on the tree examined, but on many trees the leaves were turning yellow. The bark did not separate as readily as earlier, but the cambium region still contained much water. The diameter was 3.2 inches; age 8 years.

The cambium was 4 or 5 cells wide, about 19 μ. The xylem was 1920 μ wide, on the opposite side 1395 μ, completely thickened and lignified. Cell division had ceased.

Relation of cell formation to environmental factors

The precipitation and the temperatures for the season were secured from the United States Weather Bureau. The precipitation record for the maple trees is the average of two stations, one two miles southwest of the grove, the other two miles northeast. The temperature record was secured about four miles southwest. For the ash both records were secured from the station about three miles northeast of the grove. The mean temperature and the total precipitation for periods corresponding to the intervals at which sections were taken from the trees are shown graphically in figs. 1 and 2. The width of the cambium layer on fourteen different dates was used for the growth record. Although the section for each date was taken from a different individual, the curve representing the variation in the width of this layer is an index to the rate at which new xylem cells were being formed. The wider the layer the more rapidly were new cells forming, and vice versa. The width of the xylem could not be used as a growth record because this varied too much, even in individuals growing side by side.

In order to determine the variation of the cambium layer at a certain time, the main stems of five young trees of each species were examined on December 1. In ash trees ranging from two to four years old, the width of the cambium was 3–6 cells, or 17–24 μ. The width of the 1925 xylem varied from 225 to 780 μ. In the maple trees 3–5 years old, the width of the cambium was 3–5 cells, or about 14–18 μ. The width of the 1925 xylem was 300–645 μ, so that the variation in these trees was slight.

No relation is apparent in either species between the precipitation curve and the width of the cambium. In the period preceding June 27–28, and again on August 15 when the rainfall was high (over 5 and 3 inches respectively), the rate of the production of new xylem cells remained stationary or decreased. A correlation seemed to exist between cambial activity and mean temperature. As the temperature rose above about 52° F., about April 13, cambial activity began

in the ash, and in the maple activity did not begin until about April 20, when the mean temperature had risen to 60° F. Cambial activity increased very rapidly in both species until the period May 14–27, when the mean temperature reached 65° F. As the temperature rose cambial activity declined gradually and then rapidly. In the period July 15 to August 1 the mean temperature declined from 84° to 75° and 72° F., and the width of the cambium in the maple increased from 35 to 61 μ. As the temperature went up again the cambial activity became slower, and on September 14 cell division was again proceeding accompanied by a fall in temperature.

Lignification was proceeding especially rapidly in both species after June 13, when the mean temperature was above 70° F. The June 28 ash showed that 70 per cent of the xylem formed by that time was completely lignified; in the maple about 60 per cent. Lignification in these two species appeared to be accelerated by higher mean temperatures, at least above 70° F., and cell division appeared to be favored by mean temperatures below 60° F., and retarded by higher ones.

Discussion

The maple was found to be similar to most trees (**7**, **8**, **14**) in that it did not show xylem formation until the leaves were partly expanded. The ash, however, formed new xylem before the leaves had started to expand or the branches to elongate. MACDOUGAL (**14**) states that *Fraxinus arizonica* and *Parkinsonia aculeata* are the only trees that he had encountered which showed trunk enlargement prior to shoot formation.

Early in the season there appeared to be a direct correlation between the mean temperature and cambial activity, and later the correlation appeared to be an inverse one. More study is needed before this can be established. No relation appeared evident between precipitation and cambial activity. It was not possible during the season to study the effects of other factors, such as soil temperature, soil moisture, humidity, wind, etc., but it is hoped that this will be possible in future work. There appears to be much conflicting literature on the relation of diameter increase in trees and environmental factors, but the determining factors would vary in different regions. As MACDOUGAL and SHREVE (**13**, **14**) have emphasized,

the "entire constellation of environmental factors" should be studied in relation to growth. Several individuals in each species studied should be followed throughout the season and the dendrographic method should be combined with the histological.

Summary

1. The aim of this study was to follow the course of the seasonal development of the xylem in *Fraxinus campestris* Britton and *Acer saccharinum* L. at Lincoln, Nebraska, by the histological method.

2. In the trunk of the ash, one foot high, xylem formation had started just prior to April 15, when the trees were in full bloom, and before any leaf enlargement had occurred. By April 27 the innermost row of tracheary tubes had reached maturity; by May 4 all of the large tubes were fully grown; and by May 14 all the spring wood had been formed and lignification was proceeding rapidly. The formation of new cells had decreased somewhat on June 13, and considerably so on June 28. By July 15 the summer growth had almost ceased, and over 90 per cent of the xylem was completely lignified. Renewed cambial activity was producing a few cells on August 15 on one side of the trunk, but on the other side it had not started again. On September 14 the formation of new xylem cells had ceased and lignification was complete to the cambium.

3. In the trunk of the maple, one foot high, xylem formation started in one tree just prior to April 20, and in another tree about April 27, when the leaves were about half grown. The production of new cells was very active throughout May and June, but on July 15 it had decreased considerably. By August 1 most of the season's xylem had been formed, and over 90 per cent was completely lignified. On August 15 lignification was complete to the cambium and no new cells were being produced, but on September 14 cambial activity had been renewed and new xylem cells had developed, after growth had apparently ceased for the season. By October 14 cell formation had ceased and the xylem was completely lignified.

4. On April 27 the xylem development in the ash was similar in the base of the trunk and in the 1924 and 1925 portions of the twigs, except that lignification was slightly more advanced, and the tracheary tubes were smaller and more numerous in the twigs. In the

maple on April 27 xylem formation was much further advanced in the young twigs than in the trunk, and it decreased progressively as the base was approached.

5. Cambial activity, as measured by the width of the cambium layer composed of the narrow, thin walled cells, showed no correlation with precipitation. With mean temperature, however, a direct correlation appeared to exist in the spring, until about 60° F. was reached, after which there appeared to be an inverse correlation.

COLORADO AGRICULTURAL COLLEGE
FORT COLLINS, COLO.

[*Accepted for publication December 24, 1925*]

LITERATURE

1. AUCHTER, E. C., Is there normally a cross transfer of foods, water and mineral nutrients in woody plants? Univ. Md. Agric. Exp. Sta. Bull. 257. 33–66. 1923.
2. BAILEY, I. W., The cambium and its derivative tissues. II. Size variations of cambial initials in gymnosperms and angiosperms. Amer. Jour. Bot. **7**: 355–367. 1920.
3. ———, The cambium and its derivative tissues. IV. The increase in girth of the cambium. Amer. Jour. Bot. **10**:499–509. 1923.
4. BROWN, H. P., Growth studies in forest trees. I. *Pinus rigida* Mill. BOT. GAZ. **54**:386–403. 1912.
5. ———, Growth studies in forest trees. II. *Pinus strobus* L. BOT. GAZ. **59**: 197–241. 1915.
6. EAMES, A. J., and MACDANIELS, L. H., An introduction to plant anatomy. New York. 1925.
7. GROSSENBACHER, J. G., The periodicity and distribution of radial growth in trees and their relation to the development of "annual" rings. Trans. Wis. Acad. Sci. **18**:1–77. 1915.
8. KNUDSON, L., Observations on the inception, season, and duration of cambium development in the American larch (*Larix laricina*). Bull. Torr. Bot. Club **40**:271–293. 1913.
9. KORSTIAN, C. F., Diameter growth in boxelder and blue spruce. BOT. GAZ. **71**:454–461. 1921.
10. KOSTYTSCHEW, S., Der Bau und das Dickenwachstum der Dicotylenstämme. Beih. Bot. Centralbl. **40**:295–350. 1924.
11. MACDOUGAL, D. T., Accretion and distention in plant cells. Amer. Nat. **59**:336–345. 1925.
12. ———, Growth in trees. Carnegie Inst. Wash. Publ. 307. 1921.
13. ———, Tree trunks, growth and reversible variations in circumference. Science **69**:370–372. 1925.

14. MACDOUGAL, D. T., and SHREVE, F., Growth in trees and massive organs of plants. Carnegie Inst. Wash. Publ. 350. 1924.
15. PEARSON, G. A., The growing season of the western yellow pine. Jour. Agric. Res. **29**:203–204. 1924.
16. REED, H. S., Growth and differentiation in apricot trees. Univ. Calif. Publ. Agric. Sci. **5**:1–55. 1924.
17. ROBBINS, W. J., Precipitation and growth of oaks at Columbia, Missouri. Univ. Mo. Agric. Exp. Sta. Res. Bull. 44. 1921.

EXPLANATION OF PLATES XIX–XXI

PLATE XIX

All drawings were made with the aid of a projection apparatus magnifying 600 times. All drawings show xylem, cambium, and a few phloem cells.

FIG. 1.—Ash, March 28: xylem formed in 1924; no new xylem.

FIG. 2.—Ash, April 15: xylem formation begun.

FIG. 3.—Ash, April 20: portion between thick walled 1924 xylem and cambium layer is 1925 xylem.

FIG. 4.—Ash, April 27: all xylem shown was formed in 1925; thickening and lignification of cell walls begun.

FIG. 5.—Ash, May 14: all xylem shown except upper row or two of cells was formed in 1925; spring xylem cells formed.

FIG. 6.—Ash, June 13: portion of 1924 xylem shown at upper edge of drawing; walls thickening rapidly.

FIG. 7.—Ash, June 28: total 1925 growth up to date; most of summer xylem cells formed.

PLATE XX

FIG. 8.—Ash, July 15: only portion of 1925 xylem adjacent to cambium shown, rest mature; cell division proceeding more slowly.

FIG. 9.—Ash, August 1: section from one side of trunk showing cessation of xylem formation.

FIG. 10.—Ash, August 1: section from opposite side of trunk shown in fig. 9, showing that xylem formation had started again.

FIG. 11.—Ash, August 15: very slight cambial activity; practically all xylem fully lignified.

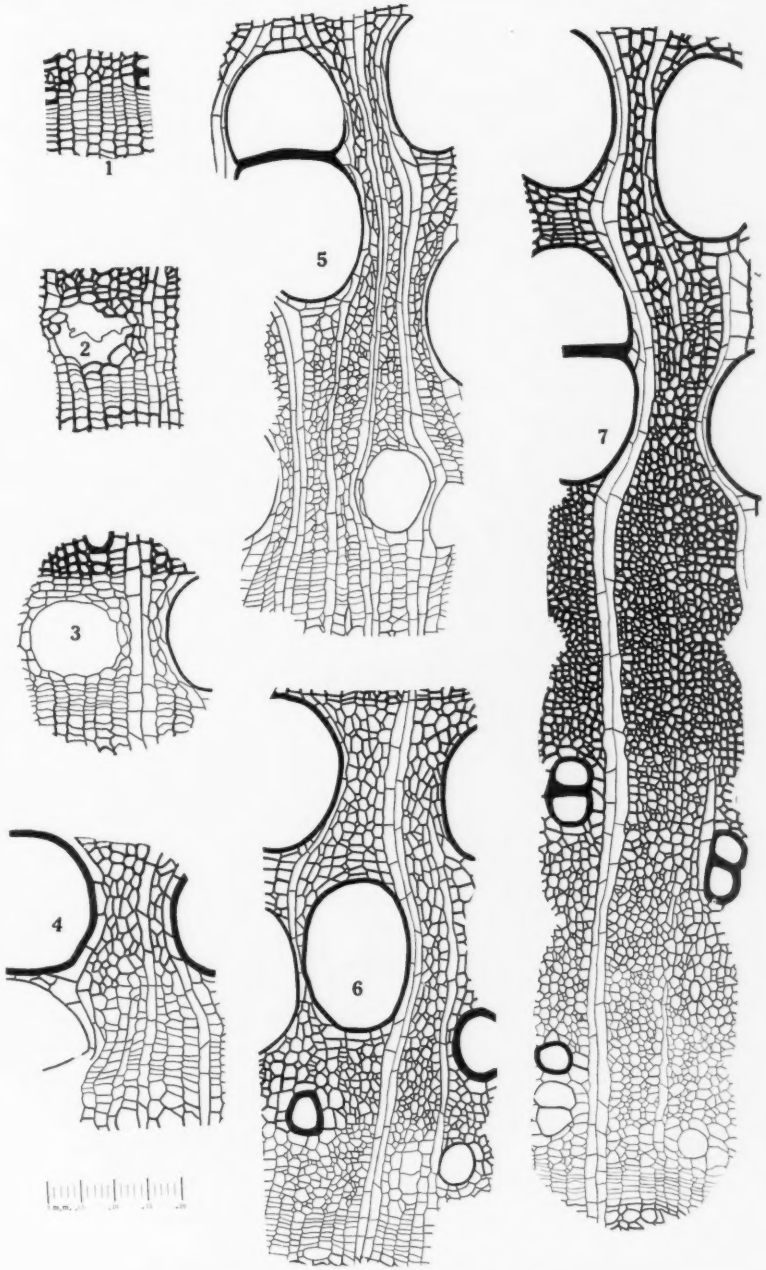
FIG. 12.—Ash, September 14: xylem fully lignified to cambium, and cell formation apparently ceased.

FIG. 13.—Soft maple, April 13: xylem formation not started.

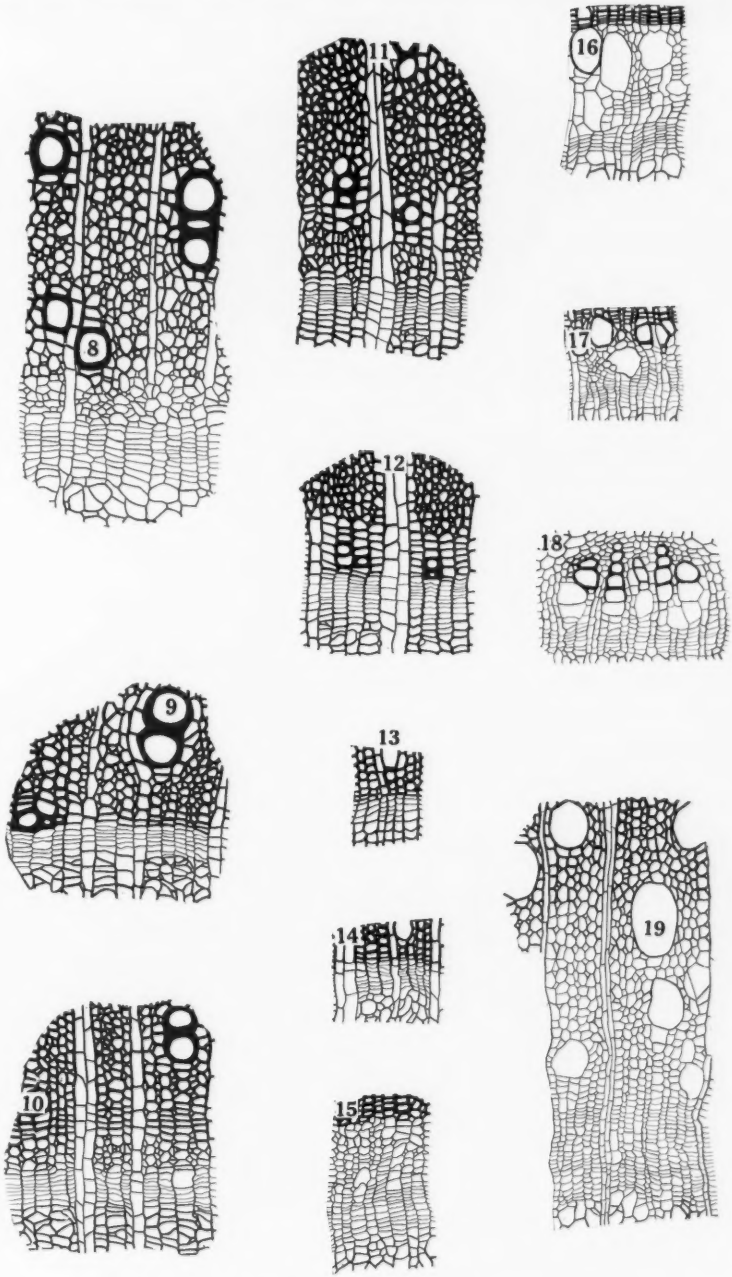
FIG. 14.—Soft maple, April 20: section from one side of trunk showing no or very slight cambial activity.

FIG. 15.—Soft maple, April 20: section from opposite side of trunk from which fig. 14 was taken showing vigorous xylem formation.

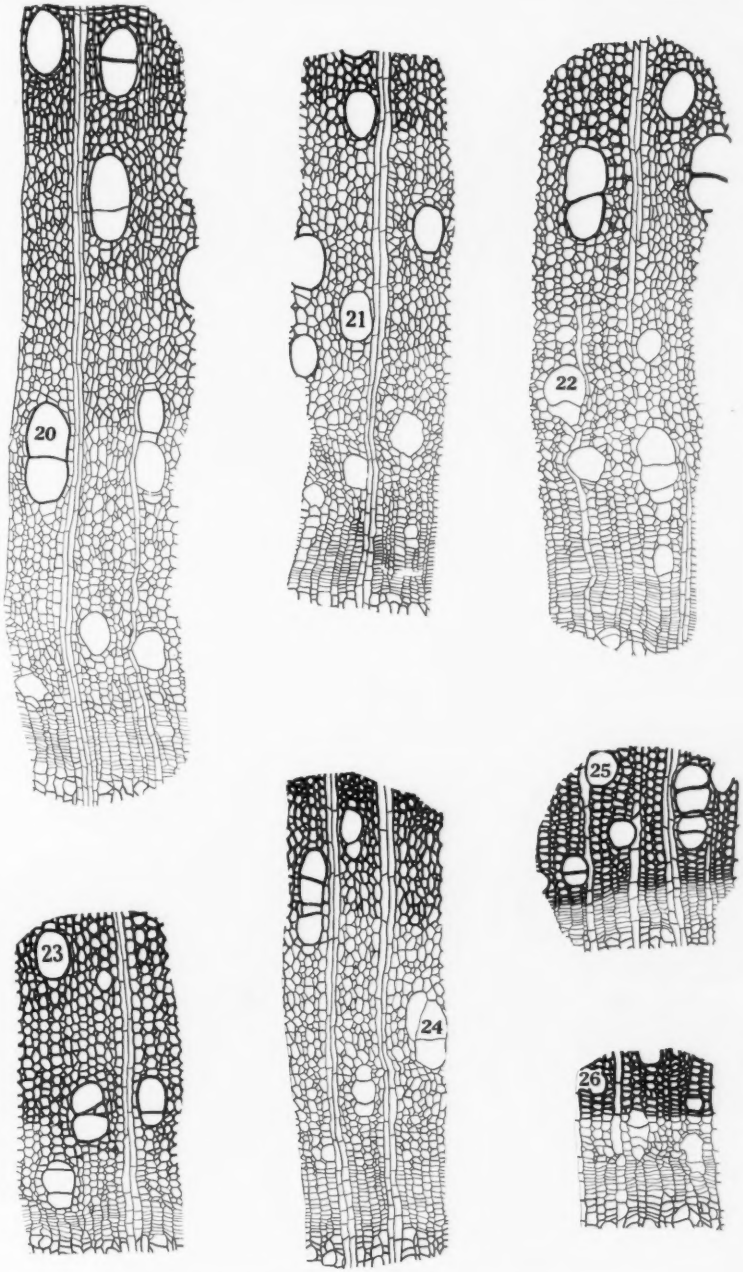
FIG. 16.—Soft maple, April 27: section from trunk at height of 18 feet showing vigorous xylem formation.



HANSON on FRAXINUS and ACER



HANSON on FRAXINUS and ACER



HANSON on FRAXINUS and ACER

FIG. 17.—Soft maple, April 27: from 1-year-old twig.

FIG. 18.—Soft maple, April 27: 1925 twig, showing xylem and cambium of medium sized bundle.

FIG. 19.—Soft maple May 7: all xylem shown was formed in 1925; thickening and lignification of walls started.

PLATE XXI

FIG. 20.—Soft maple, May 27: all xylem shown except uppermost row or two was formed in 1925.

FIG. 21.—Soft maple, June 13: portion of 1925 xylem shown.

FIG. 22.—Soft maple, June 29: portion of 1925 xylem shown; xylem formation proceeding rapidly.

FIG. 23.—Soft maple, July 15: portion of 1925 xylem shown; xylem formation has decreased.

FIG. 24.—Soft maple, August 1: portion of 1925 xylem shown; xylem formation proceeding rapidly.

FIG. 25.—Soft maple, August 15: portion of 1925 xylem shown; appearance of new cells ceased; thickening and lignification complete to cambium.

FIG. 26.—Soft maple, September 14: formation of xylem cells started anew after apparently ceasing for season.

EFFECT OF LIGHT INTENSITY ON GROWTH OF SOY BEANS AND ITS RELATION TO THE AUTO-CATALYST THEORY OF GROWTH

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 357[1]

HENRY W. POPP

(WITH EIGHT FIGURES)

Introduction

A previous study of the effect of various ranges of wave-lengths of the sun's spectrum on the growth of plants, carried out at the Boyce Thompson Institute, showed that when the Peking variety of soy beans was deprived of blue-violet rays the stems grew excessively long and twined, while plants grown under the same total light intensity but with all the rays of the sun's spectrum present gave no such response. The object of the present study was to determine whether similar effects could be produced by decreased light intensity alone, the plants receiving all rays of the sun's spectrum but at much lower intensities than were used in the previous experiment.

Materials and method

Six compartments, each 44 × 50 inches at the base and 40 inches high, were constructed inside a large greenhouse. These compartments were completely inclosed with cloth so as to give different degrees of light intensity, as indicated in table I. The light intensities were measured at different times during the day by means of a Macbeth illuminometer. The average temperature during the growth period in these compartments was 23° C. during the day and 19° at night. At no time did the temperature vary more than 1–3° C. in the different compartments. The temperature of compartment 6 was always about 1° lower than that of compartment 1.

[1] Joint contribution with the Department of Botany, Pennsylvania State College, no. 57. Published by permission of the Director of the Agricultural Experiment Station, Pennsylvania State College, no. 403.

Four varieties of soy beans were used, Peking, Mandarin, Biloxi, and Ito San. Three pots of each variety, containing four plants each, were placed in each compartment, and were so arranged as to eliminate variations resulting from different positions within the compartments. All plants were grown in 6-inch pots in the same batch of soil, a well fertilized dark sandy loam. All other conditions were kept as uniform as possible. The seeds were all sown on July 11. Weekly measurements of height were made and general observations taken on time of flowering, thickness of stems, leaf development,

TABLE I

Compartment no.	Covering	Average light intensity foot-candles (clear days)	Approximate percentage transmission of coverings (outside intensity =100 per cent)
1	None	4285	66.00
2	One layer white cheesecloth	1536	23.00
3	Two layers white cheesecloth	560	8.60
4	Three layers white cheesecloth	390	6.00
5	Four layers white cheesecloth	250	3.80
6	Two layers white cheesecloth plus one layer black calico	26	0.38

color of leaves, vigor, etc. The plants in all compartments were supported by means of bamboo canes after two weeks of growth. The experiment was continued for seven weeks.

General results

The average measurements of length of stems are given in table II and the curves of growth obtained from these data in figs. 5 to 8. Figs. 1 to 4 are photographs of the different varieties taken after six weeks of growth. The plants of compartment 6 are not shown in these photographs since they were all dead at this time.

In the early stages of growth (1–2 weeks) the rate of stem elongation in all varieties was greatest in the darkest compartment (no. 6) and least in the brightest compartment (no. 1), being in general inversely proportional to the light intensity. Gradually the majority of the plants in compartment 5 gained in rate over those of compartment 6; then those of compartment 4 gained over those of compart-

ment 5; and finally the plants of compartment 3 attained the most rapid rate of the series, with the final result that the tallest plants occurred generally in compartment 3, which had an intermediate light intensity.

TABLE II

AVERAGE HEIGHT OF PLANTS IN CM.; AVERAGE OF 12 PLANTS OF EACH VARIETY IN EACH COMPARTMENT

VARIETY	COMPARTMENT NO.						WEEKS FROM TIME OF PLANTING
	1	2	3	4	5	6	
Peking	3.61	4.40	5.18	4.66	6.72	11.02	1
Mandarin	6.40	6.32	7.35	8.90	10.61	18.75	
Biloxi	4.98	5.81	5.94	7.95	9.38	13.06	
Ito San	6.60	7.20	8.40	9.96	11.91	17.91	
Peking	8.78	10.86	15.23	16.68	17.54	26.00	2
Mandarin	13.14	13.78	17.50	23.29	24.60	37.35	
Biloxi	13.30	16.10	21.48	19.56	24.48	36.95	
Ito San	14.56	17.52	20.20	24.63	26.20	29.02	
Peking	11.90	16.16	22.33	24.61	26.28	29.07	3
Mandarin	17.92	19.60	25.90	34.75	34.55	38.59	
Biloxi	17.37	24.21	34.84	28.80	40.11	44.73	
Ito San	21.25	26.75	32.64	38.54	39.70	30.14	
Peking	19.50	25.93	40.09	39.22	34.21	29.50	4
Mandarin	27.65	26.19	38.75	46.37	40.64	Dead	
Biloxi	25.35	31.94	54.43	41.08	52.40	48.15	
Ito San	29.70	35.46	50.00	51.65	48.58	Dead	
Peking	31.58	40.85	64.83	56.31	47.78	Dead	5
Mandarin	35.90	34.80	53.80	56.48	43.75	Dead	
Biloxi	35.79	45.00	80.94	57.01	64.06	Dead	
Ito San	42.60	51.30	77.49	69.00	54.45	Dead	
Peking	42.35	59.93	90.32	73.83	57.07	Dead	6
Mandarin	41.21	37.66	57.70	58.69	44.22	Dead	
Biloxi	46.81	63.32	98.55	72.77	78.31	Dead	
Ito San	42.63	65.32	89.73	76.27	58.12	Dead	
Peking	51.08	76.79	104.40	82.50	62.10	Dead	7
Mandarin	41.37	37.68	58.18	58.74	45.16	Dead	
Biloxi	52.98	71.99	111.94	82.80	92.72	Dead	
Ito San	57.06	70.04	91.52	77.18	59.50	Dead	

There is apparently an optimum light intensity for stem elongation, which in this case was around 500 foot-candles. The falling off in rate of elongation in compartments 4 to 6 probably resulted from the inability of the plants to synthesize sufficient food to maintain rapid growth. This is evidenced by the fact that the plants of compart-

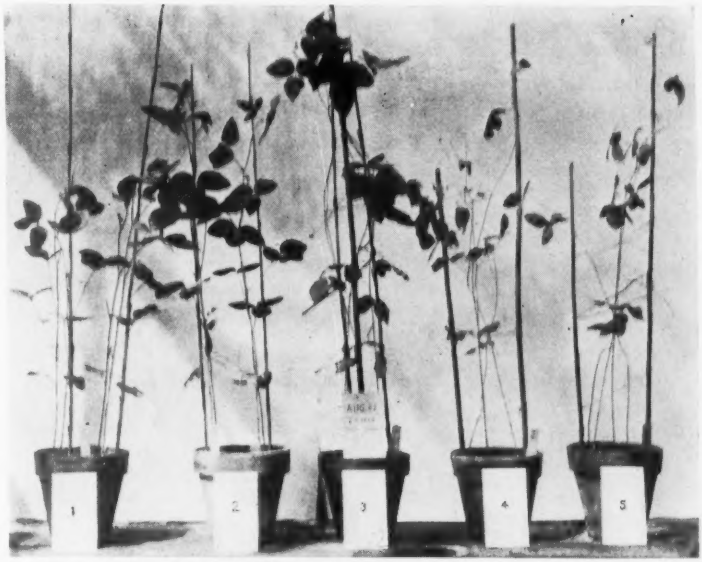


FIG. 1.—Comparison of Peking soy beans in compartments 1 to 5 (numbered from left to right).

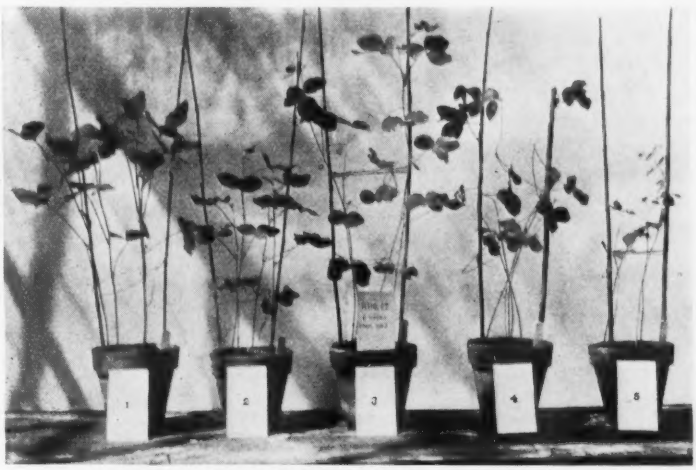


FIG. 2.—Comparison of Mandarin soy beans in compartments 1 to 5 (numbered from left to right).

ment 6 died as soon as the food in the cotyledons was depleted; in fact, these plants were almost as completely etiolated as though they had been grown in total darkness. On the other hand, the lower stature in compartments 1 and 2, under higher light intensities, was always associated with greater thickness of stems and greater

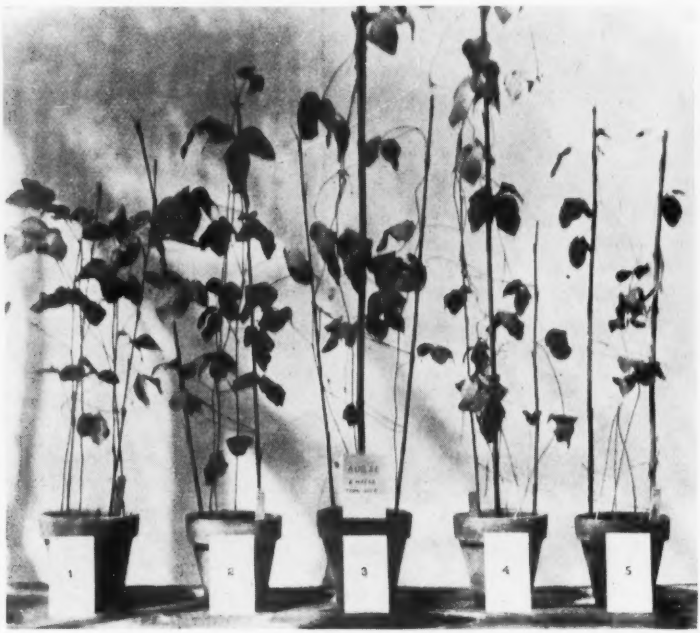


FIG. 3.—Comparison of Biloxi soy beans in compartments 1 to 5 (numbered from left to right).

size of leaves, showing that these plants had made more growth in weight than any of the others. In general the thickness and toughness of the stems were directly proportional to the light intensity, being greatest in compartment 1 and least in compartment 6. Practically all of the plants in compartments 2 to 6 were abnormally long stemmed.

There was very little difference in time of flowering in the first five compartments. The plants in each succeeding compartment be-

yond the first were about a day later in flowering than those of the preceding one. No flowering occurred in compartment 6, the plants having died before reaching that stage. Flowering began in the Mandarin variety during the fifth week, in the Ito San variety during the sixth week, and in the Peking variety during the seventh week. None

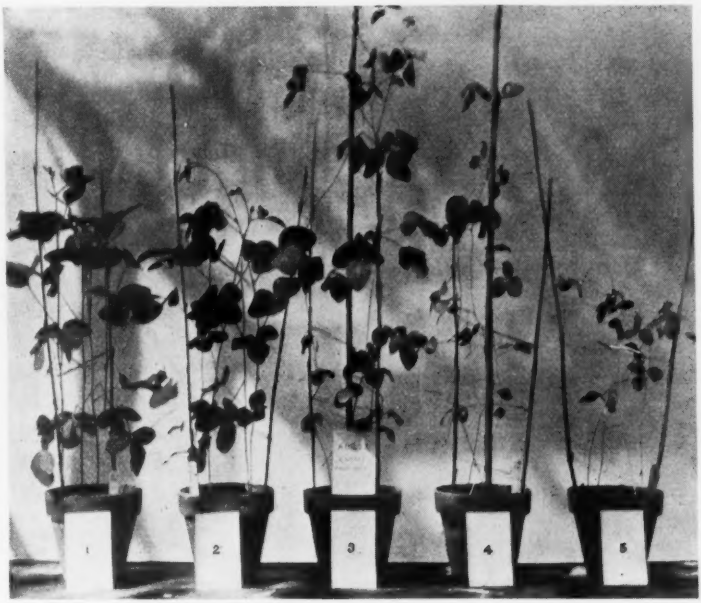


FIG. 4.—Comparison of Ito San soy beans in compartments 1 to 5 (numbered from left to right).

of the Biloxi plants had flowered by the time the experiment ended. The development of fruits decreased gradually from compartments 1 to 5. Practically no fruit developed in compartment 5.

Twining

Twining occurred in all varieties used, appearing first in compartment 5, next in compartment 4, then in compartment 3, and finally, although much less pronounced, in compartment 2. No twining occurred in any variety in compartments 1 and 6, which were

at the extremes of the series in light intensity. Apparently twining in soy beans is associated with stem length and thickness. It would appear from all studies reported and from this study that any condition that causes abnormal elongation, accompanied by decreased stem thickness or toughness, within certain limits will induce twining. The stem length necessary to induce twining is conditioned by the stem thickness, but there appears to be a minimum length of stem below which twining does not occur. In no case did any of the plants twine from the beginning of growth. The first indication of twining occurred in compartment 5 during the fourth week of growth, when the plants were 35–50 cm. high. No twining occurred in any plant before it was 35 cm. high. Twining did not occur in compartment 1, in spite of the fact that these plants attained a height of over 50 cm. and were supported in the same way as the other plants, but in this case the stems were thick and strong. On the other hand, some of the Biloxi plants in compartment 6 reached a height of 48 cm. but did not twine. In this case the stems were extremely thin and weak. Most of the plants in this compartment, however, never attained the height at which twining began in the other compartments. From the fact that the thinner stemmed plants of compartments 3 to 5 twined before the thicker stemmed plants of compartment 2, it seems that the thicker the stem, the greater must be the period of growth before twining begins.

These results seem to confirm the postulate of KLEBS, that a plant is endowed with a group of potentialities, and whether these assert themselves or not depends upon the environmental conditions under which the plants are grown. In soy beans one of these inherent tendencies seems to be toward twining. Whether twining is obtained or not depends partly upon the light conditions. The optimum for twining, however, is not the optimum for general vigor. That twining is not generally caused in plants in this way is shown by the fact that in studies of the effect of various ranges of wave-length of the sun's spectrum on the growth of plants, many other species (tomato, petunia, four o'clocks, coleus, etc.) grew to unusual length but did not twine under conditions that caused uniform twining in soy beans. In other words, there does not seem to be a latent factor for twining present in these other plants.

Rate of stem elongation and the autocatalyst theory

This study has brought out some interesting points in connection with the autocatalytic growth theory as advanced by ROBERTSON[2] and others. This theory, based on the observation that the rate of growth of an organism, when expressed in terms of height, dry weight, etc., gives a curve that is similar to the curve of a monomolecular autocatalytic reaction, assumes that growth is a catalytic process, and that the organism may be looked upon as the end product resulting from the action of an autocatalyst on a substrate. The actual configuration of the curve of growth, therefore, is thought to be caused by the activities of an autocatalyst, which, however, has not yet been identified, although several hypothetical substances have been suspected by different advocates of the theory. In a preliminary paper, MURNEEK[3] recently questions the validity of the autocatalyst theory, and gives some evidence to show that growth rate in plants can be explained on the basis of correlation. According to him the "autostatic" or later phase of the growth curve of a plant is produced "by the effects of correlation of the fruit on the rate of growth of the main stem," while the "autokinetic" phase "may probably find its counterpart of explanation in the influence of correlation of roots on the stem."

In the present study, after the curves of growth in height were plotted, it was discovered that these curves for the plants in the first five compartments (figs. 5 to 8) were similar to the curve of a monomolecular autocatalytic reaction. The similarity was most pronounced in the curves of the plants of the first three compartments, which had the highest light intensities. These plants started out at a comparatively slow rate of growth; gradually increased in rate until a maximum was reached; and finally *in those plants that flowered* fell off again. In some cases there was a slight falling off in rate between the second and third week. The plants in compartment 6, however, which had the lowest light intensity of the series, started out at a more rapid rate, maintained a fairly high rate up to the end of the second week and then fell off rapidly, thereby giving only the first part of the curve given by the other plants. It was near the time

[2] ROBERTSON, T. B., The chemical basis of growth and senescence. London. 1923.

[3] MURNEEK, A. E., BOT. GAZ. 79:329–333. 1925.

when the plants of compartment 6 died that the plants of the other compartments started on their most rapid rate of growth. It is

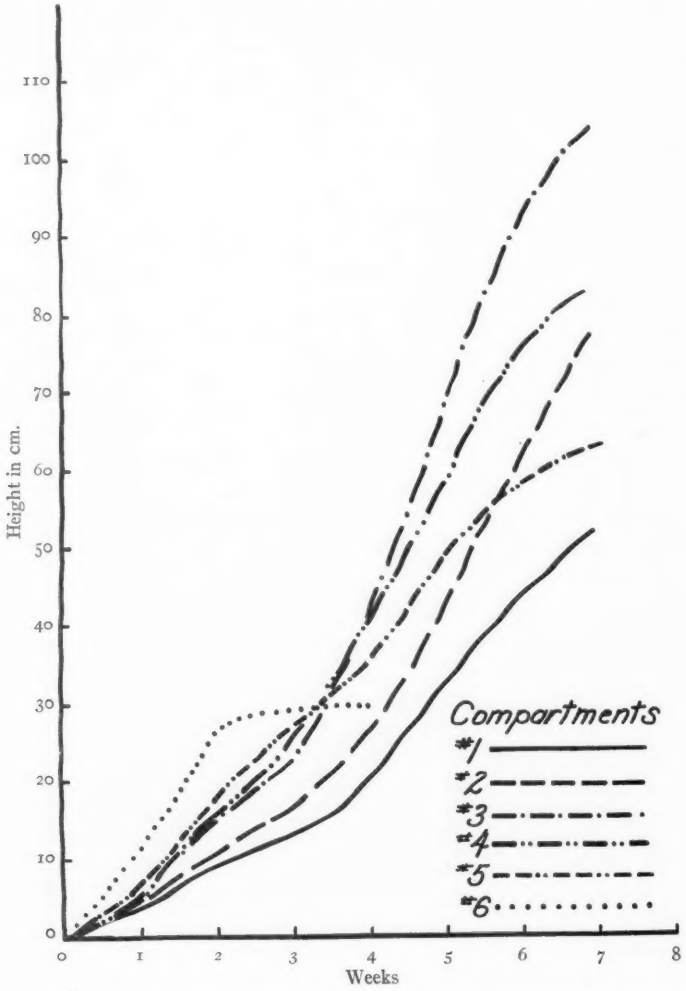


FIG. 5.—Height growth curves for Peking soy beans; plants started to flower at end of seventh week.

significant to note that this also was the time when the plants of the first five compartments began to develop mature green leaves, and therefore to manufacture enough food by photosynthesis to enable them to become independent of the food reserves in the cotyledons.

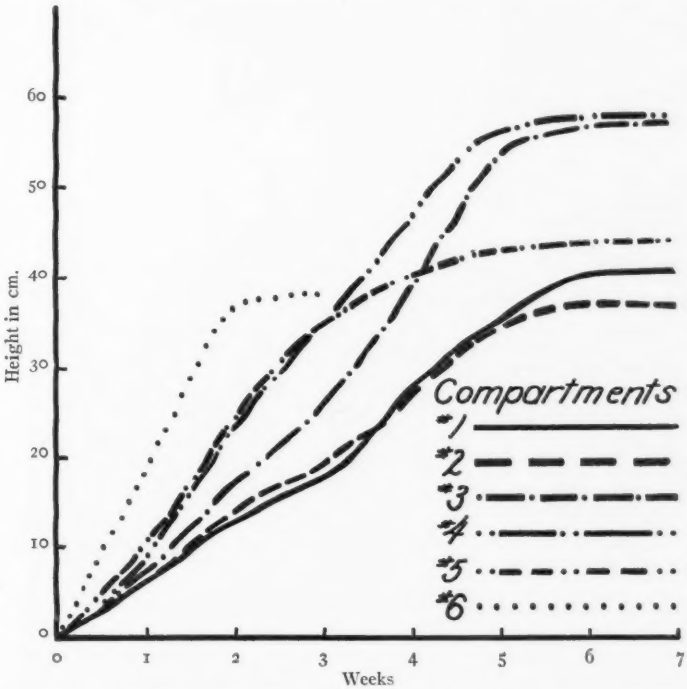


FIG. 6.—Height growth curves for Mandarin soy beans; plants started to flower at end of fifth week.

The plants of compartment 6, on the other hand, being very pale and almost completely etiolated, were unable to carry on photosynthesis to a sufficient degree to keep them alive after the reserve food of the cotyledons was depleted. The growth these plants made, therefore, represents the maximum growth that could be made from food stored in the seed, and the curve of this growth corresponds to the first part of the curves of the other plants. The configuration

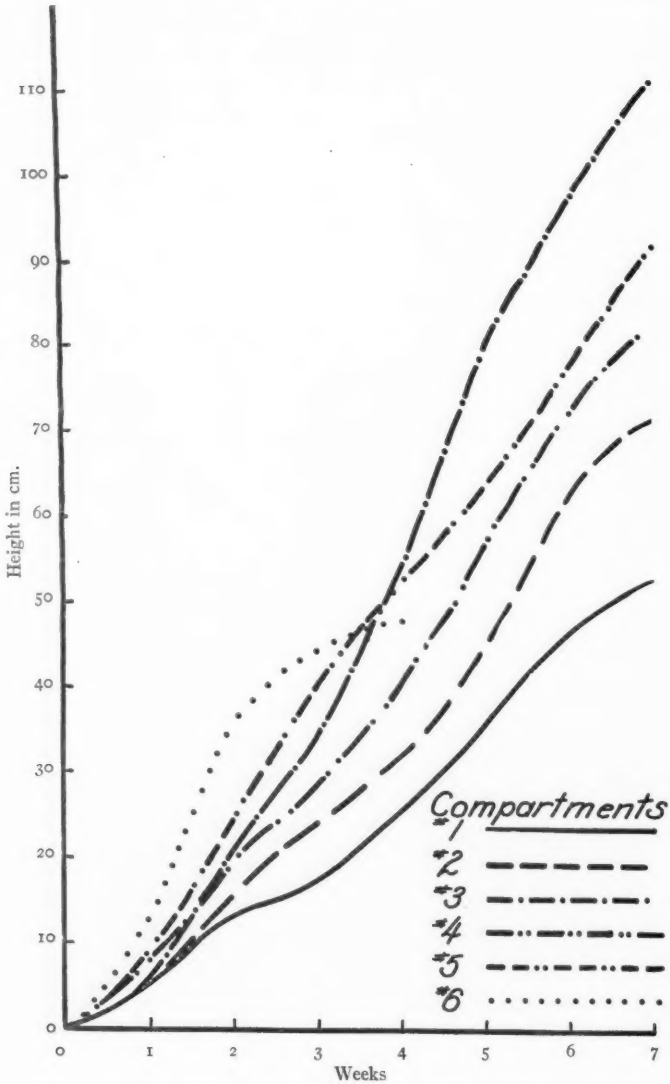


FIG. 7.—Height growth curves for Biloxi soy beans; no indication of flowering at end of seven weeks.

of the first part of these curves (autokinetic phase), therefore, appears to be associated with the initiation and development of independence in the seedling, or with the gradual ascendency of growth

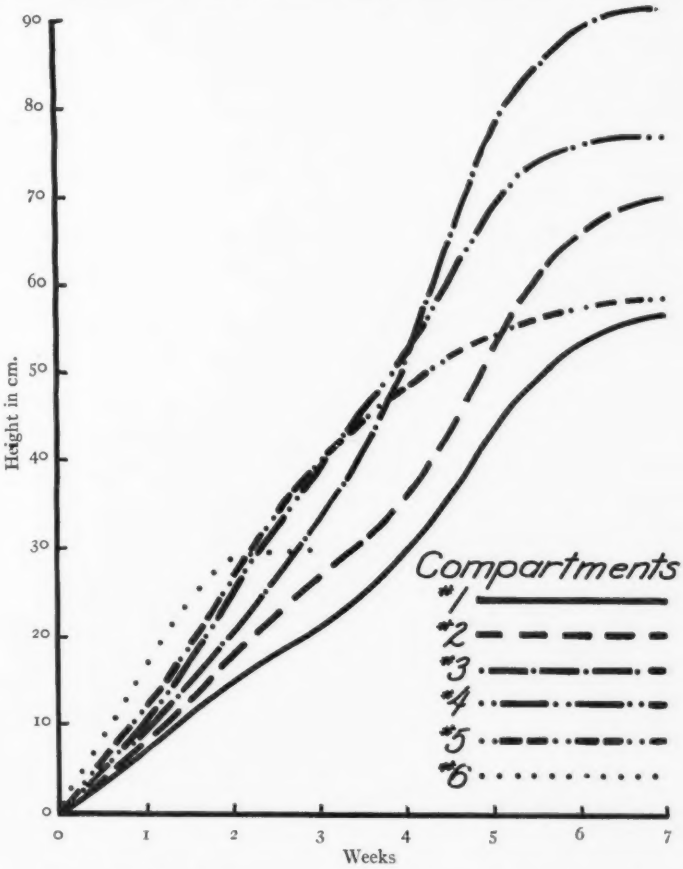


FIG. 8.—Height growth curves for Ito San soy beans; plants started to flower at end of sixth week.

resulting from food manufactured by photosynthesis over that resulting from food stored in the cotyledons. Certainly during the first part of the autokinetic phase the food is supplied by the reserves in

the seed. Since the supply is relatively large at first, the rate of growth soon becomes rapid. As the supply decreases and as more and more new tissues are made which must be supplied with food, the rate falls off unless a new and adequate supply is made by photosynthesis; but if there is sufficient light and leaf surface for photosynthesis, growth proceeds at a more rapid rate. If we examine the latter half of the curves we find that this rapid rate of growth continues so long as the plant does not flower. In all varieties that flowered, growth in length practically ceased when flowering began, while in the Biloxi variety, which did not flower, rapid growth continued. In those cases where flowering occurred, the food was apparently carried to the developing fruits and not to the growing points of the stem, and hence growth in length ceased. The falling off in rate in the "autostatic" phase of the curve, therefore, is caused by the development of flowers and fruit. This last point is exactly in accord with the facts MURNEEK pointed out.

While this study does not in any way prove the absence of an autocatalyst, yet it shows that it is possible to interpret the configuration of the curves of growth on a more tangible basis than to assume the presence of hypothetical substances.

Summary

The effect of different light intensities on the growth of soy beans was studied by growing four different varieties under six different light intensities, averaging 4285, 1536, 560, 390, 250, and 26 foot-candles respectively. The results were as follows:

1. The lower the light intensity, the more rapid was the rate of stem elongation during the initial period of growth.

2. The greatest general height was attained by plants under a light intensity averaging 560 foot-candles, and the lowest under an average intensity of 26 foot-candles.

3. The thickness of the stems was directly proportional to the light intensity, being greatest under 4285 foot-candles and least under 26 foot-candles.

4. In general all of the plants were unusually long stemmed. Those receiving the greatest amount of light were the most vigorous, produced the best leaves and color, and the best fruit. There was a

gradual decrease in vigor, etc., with decreasing light intensity. Plants grown under 26 foot-candles were completely etiolated and died within three to four weeks.

5. Twining occurred in all plants under light intensities between 250 and 1536 foot-candles, but not under 4285 foot-candles nor under 26 foot-candles. Soy beans apparently have a latent factor for twining which is associated with stem length and thickness. Thick stems require a greater length for twining than thin ones, but in no case did twining occur in a stem less than 35 cm. high.

6. The curves of growth in length of all plants except those in the darkest compartment followed the general curve of a monomolecular autocatalytic reaction. The autokinetic phase of the curves appeared to be associated with the initiation and development of independence in the seedling brought about by the ascendency of photosynthesis, while the falling off in rate during the latter part of the autostatic phase was caused by the development of flowering and fruiting.

The writer desires to acknowledge his indebtedness to Professor C. A. SHULL for his interest and helpful suggestions in this work.

PENNSYLVANIA STATE COLLEGE
STATE COLLEGE, PA.

[*Accepted for publication January 18, 1926*]

EFFECT OF CERTAIN DEFICIENCIES ON NITROGEN METABOLISM OF PLANTS

R. C. Burrell

Introduction

Very little is known concerning protein synthesis in plants. The intermediate steps involved in the building of these compounds from the simple plant nutrients have never been satisfactorily worked out.

There is evidence that some of the mineral elements recognized as essential for plant growth play important rôles in certain stages of the protein synthesis. For example, Scruti (5) has attributed to phosphorus an important rôle in higher plants in the formation of the amino acids; and recently, Kraybill (4) has obtained some interesting results in an extensive study of the relation of phosphorus to the nitrogen metabolism of the tomato. Limiting the available quantities of such elements should throw the ordinary leaf machinery out of gear, permitting certain intermediate products of protein synthesis to accumulate, while other substances would cease to be formed, or at least would be produced in only abnormally small amounts. If lack of a certain mineral element, as calcium, would retard or stop the protein synthesis at a different stage from that caused by the lack of some other essential element, as potassium, then intermediate products of varying degrees of complexity might be determined; also some definite functions of these essential elements would be established.

In this investigation the effects of magnesium, potassium, and calcium deficiency on the composition of certain plants were studied. The analyses were compared with analyses of control plants grown side by side with the deficient plants, but supplied with all the essential nutrient elements.

Experimental procedure

Soy beans (Peking) and pumpkins (Connecticut Field) were the plants selected for the experiments, because they were found to make a rather rapid growth and to thrive moderately well in the green-

house. Navy beans were tried at first, but when grown in sand cultures they were found to be very susceptible to a bacterial wilt, apparently carried by the seed. The plants were grown in trays filled with washed quartz sand. The bottoms of the trays were brushed over on the inside with melted paraffin, the moist sand put in, and the seeds planted in rows three inches apart and one-half inch apart in the rows. Subsequent watering was carried out with the diluted nutrient solutions described later. As required, the same quantities were added to each tray in the same way.

To take into account the effect of greenhouse conditions and other factors that could not be definitely controlled, the trays were alternated with trays of control plants on the greenhouse bench. The development and composition of the deficient plants and of the control plants were then compared. Since all external conditions were approximately the same in the cases of the plants compared, except that one element was deficient, the differences observed were assumed to be due to this deficiency.

Five days after the seedlings appeared above ground, the cotyledons were removed in order that the effects of the deficiency might appear sooner. Thirty days after this (35 days above ground) the plants were sampled. Definite numbers of average plants were removed from the deficient and control trays and stripped of their leaves (petioles removed). These leaf samples were then weighed and preserved in 80 per cent alcohol, with the addition of calcium carbonate, as later described. The stems, from the roots to the point of attachment of the cotyledons, were preserved similarly as separate samples.

The nutrient solutions used were similar to those employed by DICKSON (2), except that they were recalculated to an absolute deficiency of the element in question, instead of merely reducing it to one-tenth of that in the normal solution used. This is essentially Knop's solution, diluted one to ten, with corresponding deficient solutions containing exactly the same physiological balance of all the other essential elements except the one that is lacking. The dilution is necessary to take care of the accumulation of salts in sand cultures watered with nutrient solutions. Chemically pure reagents were used. Calcium nitrate and magnesium sulphate solutions were pre-

pared by making approximate solutions from the hydrates, determining the concentration of calcium and magnesium in each by analysis, and then making appropriate dilutions. A block tin condenser was used in the preparation of the distilled water, and solutions were stored in seasoned alkali treated flint glass bottles. Stock solutions of the various salts were prepared which served during the whole experiment. The hydrogen-ion concentrations of the diluted solutions, as actually applied to the plants, varied between 4.5 and 5.0 P_H. The osmotic pressure of each solution was approximately 0.0151; that of the calcium deficient solution was very slightly

TABLE I

CONCENTRATIONS OF SALTS IN NUTRIENT SOLUTIONS (GM. PER LITER)

	NORMAL	Mg DEFICIENT	K DEFICIENT	Ca DEFICIENT
Calcium nitrate	0.533	0.533	0.533	.....
Potassium nitrate	0.133	0.133	.....	0.133
Potassium phosphate	0.133	0.133	.....	0.133
Magnesium sulphate	0.133	.....	0.133	0.133
Sodium chloride	0.067	0.070	0.063	.....
Sodium nitrate	.....	.....	0.111	0.552
Sodium sulphate	.....	0.1576	.....	.....
Sodium phosphate	.....	.....	0.117	.....

higher. The concentrations of the diluted solutions are given in table I. Two and five-tenths cc. M–100 ferric chloride solution was added to each liter of nutrient solution just before applying to the plants.

When the plants had grown 35 days above ground, they were sampled as described. Sufficient data were recorded so that the composition of the plants could be expressed in several ways (fresh weight, dry weight, and per plant). Cotyledons, leaves, and stems were sampled separately. The sample, 50–100 gm. weighed accurately to one decigram, was cut in small pieces with a pair of scissors. Five-tenths of a gram of calcium carbonate (ppt. chalk) was sprinkled over it to neutralize the acidity of the solution, which would cause the inversion of sucrose and other changes; sufficient 95 per cent aldehyde free alcohol and water was added to bring the final concentration of alcohol to 80 per cent. The mixture was heated rapidly to boiling on the steam bath to stop enzyme action, and set

aside, carefully covered, for a day or longer. The liquid was then decanted off, filtered through a hardened filter, and the residue dried at 105° and pulverized. The powdered material was placed in a Vivian extractor and extracted with some of the alcoholic filtrate until the percolate was colorless. The volume of the total extract was made up to 1 liter with 80 per cent alcohol, and aliquots of this solution were used in the determination of the various soluble nitrogen and carbohydrate compounds, as follows:

Chemical analyses of samples

SUBSTANCE DETERMINED

1. Insoluble residue	5. Nitrate nitrogen	9. Amino acid nitrogen
2. Solids in extract	6. Nitrites	10. Reducing sugars
3. Insoluble nitrogen	7. Ammonia nitrogen	11. Sucrose
4. Soluble nitrogen	8. Amide nitrogen	12. Starch

METHODS

1. INSOLUBLE RESIDUE.—The material remaining from the final alcoholic extraction of the leaf tissue was dried at 100° C. and corrected for the added calcium carbonate.

2. SOLIDS IN EXTRACT.—Fifty cc. aliquots of the alcoholic extract were evaporated and the residue dried at 100° C.

3. INSOLUBLE NITROGEN.—The determination was made by the Kjeldahl process, on 1 gm. samples of the dried residue from the extraction. These were ground to pass through an 80 mesh sieve.

4. SOLUBLE NITROGEN OF EXTRACT.—Total nitrogen, including nitrates (preliminary reduction with Devarda's alloy), was determined, using 50 cc. aliquots of the alcoholic extract.

5. NITRATE NITROGEN.—This was determined by the phenol di-sulphonic acid colorimetric method as modified by BURRELL and PHILLIPS (1).

6. NITRITES.—Aliquots of the alcoholic extract were treated as in the nitrate determination, up to the point of being oxidized with sodium peroxide. At this stage they were neutralized with sodium hydroxide solution, and nitrites were determined colorimetrically, using the alpha naphthyl amine-sulphanilic acid reagent.

7, 8. AMMONIA AND AMIDE NITROGEN.—The Van Slyke Cullen urea apparatus was used, the ammonia being liberated by 52 per

cent potassium carbonate solution. Aeration was carried on for one hour into 0.02 N acid. Blanks were run simultaneously and the ammonia determined by titration. For amide nitrogen, the sample was subjected to a preliminary amide hydrolysis, and the total ammonia nitrogen was then found as previously described. Subtracting the ammonia nitrogen previously found present as such, gave the amide nitrogen.

9. AMINO ACID NITROGEN.—This was determined by the Van Slyke method, using the micro apparatus.

10. REDUCING SUGARS.—Picrate reduction and colorimetric estimation were used. The sample was prepared by the method recommended by THOMAS and DUTCHER (7). Analysis of the clear filtrate, however, was carried out by the method as described by WILLAMAN and DAVISON (8), making use also of their correction tables.

11. SUCROSE.—Part of the clarified filtrate from "reducing sugars" was treated by the standard Herzfeld procedure, and a determination of total sugars carried out by the method used for reducing sugars. Making use of the appropriate corrections in WILLAMAN and DAVISON'S paper, sucrose was calculated.

12. STARCH.—Two gram samples of the dried extracted residue were subjected to starch determinations according to the method of THOMAS (6).

Discussion

MAGNESIUM DEFICIENCY.—Magnesium deficient plants were not noticeably different in appearance from the controls (table II). A very small supply of magnesium (largely derived from the cotyledons before they were removed) seemed sufficient for the usual development of the chlorophyll and growth of the plant for the 35-day periods used in these experiments. Some navy bean plants which were grown to the blossoming stage, however, did show a much decreased vigor and the leaves were lighter in color than those of the controls. There is not a great difference in chemical composition between the magnesium deficient and control plants. In general, the quantity of starch is slightly less in the magnesium deficient plants in both leaves and stems; soluble nitrogen is slightly greater in the leaves of the magnesium deficient plants and about the same in the stems; and insoluble nitrogen is consistently slightly less in both the

TABLE II

ANALYSES OF NORMAL AND DEFICIENT SOY BEAN TISSUES; FRESH WEIGHT BASIS
MAGNESIUM DEFICIENCY

TISSUE	AGE IN DAYS	NO. OF PLANTS USED	FRESH WEIGHT (GM.)	PERCENTAGE												NITRITES
				Insoluble residue	Solids soluble 80 per cent alcohol	Dry matter	Insoluble nitrogen	Soluble nitrogen	Nitrate nitrogen	Ammonia nitrogen	Amide nitrogen	Amino acid nitrogen	Reducing sugars	Sucrose	Starch	
Cotyledons.....	5	500	93.1	9.84	3.35	13.19	0.626	0.167	.....	0.0016	0.0300	0.080	0.32	0.10	0.38	+
Normal leaves....	35	200	106.9	11.92	3.76	15.68	0.553	0.141	0.021	0.0002	0.0082	0.031	0.24	0.36	0.34	++
Deficient leaves..	35	200	100.55	11.18	3.24	14.42	0.470	0.163	0.024	0.0002	0.0052	0.042	0.21	0.30	0.29	++
Normal stems....	35	200	60.9	10.59	1.80	12.39	0.189	0.097	0.039	.....	0.0086	0.014	0.30	0.05	0.18	+
Deficient stems...	35	200	52.0	10.39	1.85	12.24	0.172	0.093	0.039	.....	0.0101	0.010	0.22	0.04	0.13	+

TABLE III

ANALYSES OF NORMAL AND DEFICIENT SOY BEAN TISSUES; FRESH WEIGHT BASIS
POTASSIUM DEFICIENCY

TISSUE	AGE IN DAYS	NO. OF PLANTS USED	FRESH WEIGHT GM.	PERCENTAGE												NITRITES
				Insoluble residue	Solids soluble 80 per cent alcohol	Dry matter	Insoluble nitrogen	Soluble nitrogen	Nitrate nitrogen	Ammonia nitrogen	Amide nitrogen	Amino acid nitrogen	Reducing sugars	Sucrose	Starch	
Cotyledons.....	5	550	100.0	8.80	2.94	11.74	0.532	0.153	.....	0.0018	0.032	0.071	0.28	0.15	0.32	+
Normal leaves....	35	200	111.0	12.07	2.93	15.00	0.489	0.125	0.020	0.0002	0.005	0.045	0.24	0.28	0.30	++
Deficient leaves..	35	200	100.6	12.22	3.46	15.68	0.442	0.147	0.023	0.0003	0.008	0.062	0.20	0.30	0.52	++
Normal stems....	35	200	81.2	12.31	1.86	14.17	0.233	0.078	0.025	.....	0.013	0.022	0.26	0.06	0.24	+
Deficient stems...	35	200	69.6	11.07	2.15	13.22	0.167	0.083	0.028	.....	0.015	0.025	0.15	0.07	0.14	+

TABLE IV

ANALYSES OF NORMAL AND DEFICIENT SOY BEAN TISSUES; FRESH WEIGHT BASIS

CALCIUM DEFICIENCY

TISSUE	AGE IN DAYS	NO. OF PLANTS USED	FRESH WEIGHT (GM.)	PERCENTAGE												NITRITES
				Insoluble residue	Solids soluble 80 per cent alcohol	Dry matter	Insoluble nitrogen	Soluble nitrogen	Nitrate nitrogen	Ammonia nitrogen	Amide nitrogen	Amino acid nitrogen	Reducing sugars	Sucrose	Starch	
Cotyledons	5	500	100.0	9.08	2.94	12.02	0.588	0.158	0.008	0.022	0.040	0.083	0.35	0.12	0.21	++++
Normal leaves	35	184	100.0	11.54	3.81	15.35	0.527	0.131	0.026	0.008	0.007	0.046	0.28	0.33	0.31	++++
Deficient leaves	35	252	100.0	11.83	4.28	16.11	0.344	0.108	0.049	0.0066	0.010	0.029	0.31	0.35	0.33	++
Normal stems	35	184	67.5	12.03	1.87	13.90	0.212	0.077	0.031	0.0004	0.011	0.019	0.21	0.08	0.27	++
Deficient stems	35	252	52.0	9.69	2.46	12.12	0.142	0.061	0.036	0.0005	0.006	0.013	0.23	0.13	0.15	

stems and leaves of the magnesium deficient plants. There are many other slight variations in the quantities of the various substances determined, but these are quite apparent from the table. They are hardly sufficiently marked to justify any hypotheses to explain them until more data of this kind have been accumulated. Nodules were not developed on the roots of the soy beans in any of the experiments.

POTASSIUM DEFICIENCY.—Plants grown under a deficiency of potassium differed considerably in physical appearance from the controls (table III). The leaves and stems were a different shade of green, and many of the leaves were blotched with lighter shades. Over 50 per cent of the potassium deficient pumpkin plants died from a bacterial infection during the seedling stage; none of the control plants grown side by side with these were so affected. The most noticeable difference in chemical composition between potassium deficient and control plants is the accumulation of starch in the leaves of the former. In the stems, how-

ever, starch is less with the potassium deficient plants than with the controls. HARTWELL (3) has also observed a similar condition, while WIMMER (9) found a failure to produce sugar and starch with potassium deficient plants, but this may vary with the stage of development. The percentage of dry matter is slightly higher in the potassium deficient than in control leaves. Insoluble nitrogen is less in all cases in both the stems and leaves of the potassium deficient plants; soluble nitrogen is greater; and amino acid nitrogen is especially high as compared with the quantity present in control plants. Potassium seems to have some function in the translocation and utilization of starch, and to be of especial importance in the formation of proteins from carbohydrates and amino acids.

CALCIUM DEFICIENCY.—Calcium deficient plants differed more markedly from the controls than did the potassium or magnesium deficient plants (table IV). The calcium deficient plants were smaller, of a yellow color, and showed less root development than the controls. When the sand in the trays had dried slightly, the roots of the calcium deficient plants could be pulled up with ease, while the control plants could not. The roots of the calcium deficient plants were noticeably brownish in color, especially on drying, and many were losing their epidermis. ECKERSON noted a similar condition in plants grown in water cultures deficient in calcium, and explained it by assuming that insoluble calcium pectate was normally present, but that with the calcium deficient plants the calcium was replaced by magnesium and other ions to form soluble pectates. The most striking feature of the chemical composition is the accumulation of nitrate in the leaves of the calcium deficient plants. Insoluble nitrogen is considerably less and amino acid nitrogen is less in both the leaves and stems of the calcium deficient plants. Calcium may play some important rôle in nitrate reduction, although, as previously stated, caution must be observed against drawing too sweeping conclusions until more data can be accumulated.

Conclusions

The use of deficient nutrient solutions for studying processes concerned in plant metabolism has been shown to have considerable possibilities. In these preliminary experiments the idea suggested at

the beginning of this paper was confirmed, namely, that certain elements play important rôles in different stages of synthesis occurring in plants. Also, when a certain essential element is markedly lacking, a process, as protein synthesis, may be greatly retarded at a certain stage, so that an abnormal accumulation of some intermediate product results. The products characteristic of the later stages of the synthesis are formed in abnormally small quantities.

Thanks are due to Dr. T. G. PHILLIPS of the University of New Hampshire, and to Dr. E. N. TRANSEAU of Ohio State University for many helpful suggestions during the course of this investigation.

OHIO STATE UNIVERSITY
COLUMBUS, OHIO

[*Accepted for publication November 5, 1925*]

LITERATURE CITED

1. BURRELL R. C., and PHILLIPS, T. G., The determination of nitrate nitrogen in plants. Jour. Biol. Chem. **65**:229. 1925.
2. DICKSON, J. C., The value of certain nutritive elements in the development of the oat plant. Amer. Jour. Bot. **5**:301. 1918. *ibid.* **8**:256. 1921.
3. HARTWELL, B. L., Starch congestion accompanying certain factors which retard plant growth. R.I. Agric. Exp. Sta. Bull. 165. 3. 1916.
4. KRAYBILL, H. R., N.H. Coll. Agric. Report Bull. 212. 1924 (and unpublished work).
5. SCRUTI, F., Phosphorus and the forming of amino acids in higher plants. Staz. Sper. Agrar. Ital. **41**:456. C.A. **3**:763. 1909.
6. THOMAS, W., The colorimetric determination of carbohydrates in plants by the picric acid reduction method (starch). Jour Amer. Chem. Soc. **46**:1670. 1924.
7. THOMAS, W., and DUTCHER, R. A., The colorimetric determination of carbohydrates in plants by the picric acid reduction method. Jour. Amer. Chem. Soc. **46**:1662. 1924.
8. WILLAMAN, J. J., and DAVISON, F. R., Modification of the picric acid method for sugars. Jour. Agric. Res. **28**:479. 1924.
9. WIMMER, S., Kalimangelerscheinungen an Pflanzen und Kaliersatzdunger. Chem. Ztg. **35**:1256. 1911.

CARPELOID STAMENS OF PODOPHYLLUM PELTATUM

M. Louise Sawyer

(WITH FIVE FIGURES)

During the spring of 1919, on bringing into the botanical laboratory of Grinnell College, Iowa, a large collection of *Podophyllum peltatum*, taken in a country pasture and intended for class study, the writer found a number of abnormal flowers. These seemed to be sufficiently interesting to be worth investigating.

In these flowers (fig. 1) the pistil was quite normal and the floral envelopes practically so, although showing a slight tendency to have more than the usual number of petals. The unusual parts were the stamens. These organs were greatly enlarged at the apex by the occurrence, at the end of an expanded elongation of the connective, of a well developed stigmatic surface, closely resembling that borne normally on the pistil. These stamens with their terminating stigmas were of varying forms, and were found to bear not only pollen sacs containing pollen grains, but most of them also bore ovule-like structures of varying sizes and shapes. On many of the stamens the connective expansion was more or less like an open fan in shape, and the thickly convoluted margin was stigmatic (fig. 2). The ovules of these stamens were usually borne on the lower part of the expanded portion, not far from the pollen sacs. Other stamens bore disk-shaped enlargements with the stigmatic convolution surrounding the entire disk, except for an occasional interruption in the lower part near the pollen sacs. Often the spot not occupied by stigmatic tissue bore an ovule. Again, some of the stamens gave rise to several hornlike projections, each with stigmatic tissue at its tip. The most interesting variation in the form of the connective expansion was found on a few stamens which ended in a hoodlike structure that nearly inclosed a cavity. This condition is suggestive of an ovary. Such a stamen is discernible at the upper part of the stamen whorl in fig. 1. The ovules on these structures were located near the opening of the cavity, and the stigmatic surface was confined to the margin of the

tissue which surrounded the lacuna. Some of the stamens of this type lacked pollen sacs (fig. 3).

Ovuliferous stamens similar to those here reported have long been known. WORSDELL[1] figures, somewhat diagrammatically, a section throughout the stamens of *Papaver rhalis* var. *commutatum*, showing a proximity of pollen sacs and ovule-like structures comparable with that found in this material of *Podophyllum*, but, so far as the writer knows, such reports do not include findings on the internal structure of the unusual ovules. This investigation was undertaken for the purpose of determining whether these bodies had the internal structure of ovules.

FIG. 1.—*Podophyllum* flower with abnormal stamens.

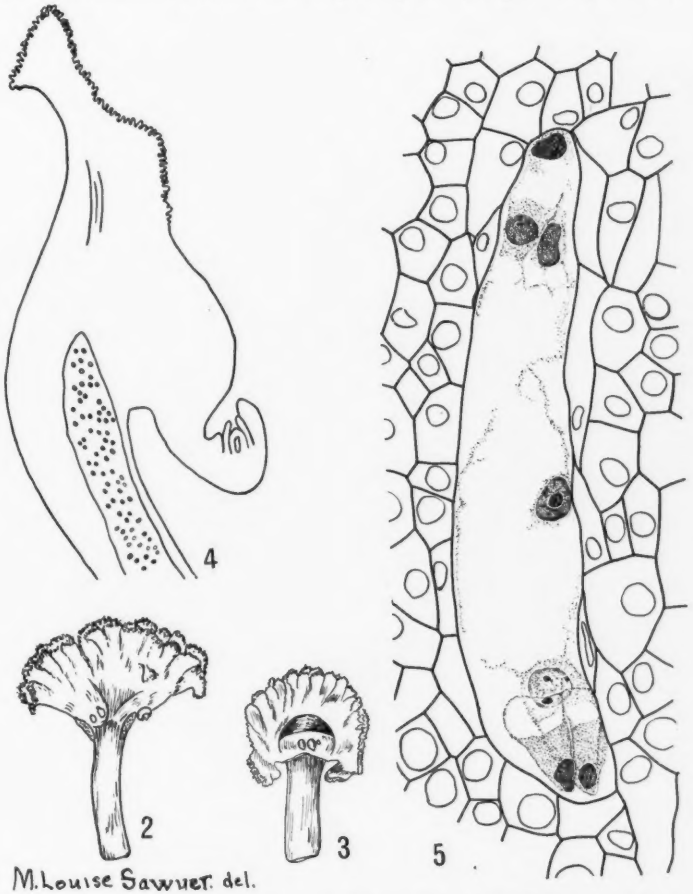
The material was fixed in a modification of Flemming's stronger solution and imbedded in paraffin. Serial sections were made and stained in Haidenhain's iron-haematoxylin.

Sections were obtained showing the relative positions of stigmatic tissue, ovules, and pollen sacs with the pollen grains (fig. 4). The pollen grains have the usual structure. They contain a recognizable generative cell and a tube nucleus, and appear wholly normal. Further, the ovule-like bodies were found to have the essential structure of ovules, but differed somewhat widely in the stage of development which they had attained, ranging from those showing a nucellus but partly enveloped by the integuments, to ovules with fully organized embryo sacs.

Some ovules show the nucellus containing an embryo sac and enveloped by the inner integument, the outer integument represent-

[1] WORSDELL, W. C., Principles of plant teratology. Vol. II. pp. 185–193, 1915.

ed only by an irregular collar at the base of the ovule. In some there is a nucellus more or less enveloped by the integuments, but con-



FIGS. 2–5.—fig. 2, one of the unusual stamens, bearing pollen sacs, ovules, and stigmatic tissue; fig 3, one of the unusual stamens, terminated by a hoodlike expansion which forms a nearly closed ovary-like cavity, with ovules borne near the opening; fig. 4, section through one of the unusual stamens showing stigmatic surface, ovule, and pollen sac containing pollen grains; fig. 5, mature embryo sac from an ovule borne on one of the unusual stamens.

taining no embryo sac. One series of sections gives an ovule with an embryo sac at the 2-nucleate stage. Another series of sections

shows an embryo sac in which the eight nuclei are evident and the polar nuclei are seen in contact, but antipodal nuclei have not organized cells, and at the micropylar end the egg apparatus is not developed, although the three cells are there. Still others reveal a mature embryo sac in which polar fusion seems to have occurred and the egg apparatus has the usual configuration (fig. 5).

Here, then, are sporophylls bearing both microsporangia and megasporangia. The microsporangia produce microspores which appear to become normal pollen grains, and the megaspores may give rise to normal embryo sacs, judging by the appearance of these structures in the sections. It would have been interesting to hand pollinate the unusual stigmas and attempt to secure ripe seeds on these carpeloid stamens. Unfortunately it was found that all of the unusual flowers in the sporting colony had been gathered. Had the writer been in the same locality another spring, an attempt to secure such results would have been undertaken, if the unusual flowers had been found a second season. BRONGNIART[1] reports a flower of *Pelemonium caeruleum* in which the stamens were represented by a circle of carpels around the central ovary, and by artificial fertilization he obtained fertile seeds from both the normal ovary and the surrounding metamorphosed stamens. It seems not unlikely that artificial pollination of the unusual *Podophyllum* material might have been followed by similar results.

There remains the interesting question whether there is a difference in the chromatic content of the usual egg and sperm in plants. If such a difference normally occurs, does it occur in the egg and sperm derived from these "bisexual" stamens, and at what point does the differentiation take place? Unfortunately the material contained no division stages, and suggests no answer to this problem, other than to indicate that if there are differences they must arise later than the differentiation of stamens and carpels, since here are stamens which give rise to both microspores and megaspores.

WELLESLEY COLLEGE
WELLESLEY, MASS.

[*Accepted for publication August 5, 1925*]

[1] BRONGNIART, A. T., Bull. Soc. Bot. France **8**:453. 1844.

COSMOS BLAKEI, A NEW SPECIES FROM GUATEMALA

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 358

EARL EDWARD SHERFF

(WITH PLATE XXII)

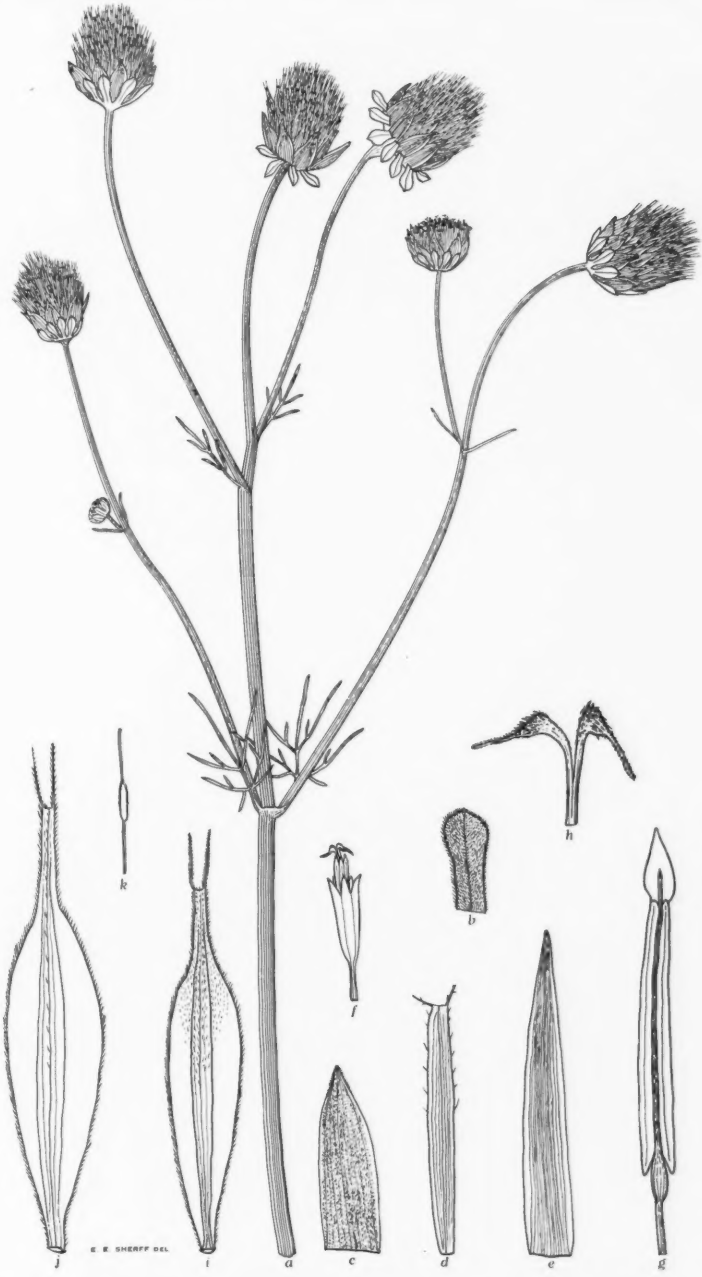
Among the interesting Guatemalan plants collected a half century or more ago by BERNOULLI and CARIO was their no. 1476. This was determined, with a mark of interrogation, as being a specimen of *Coreopsis*, and under that name the Kew specimen has lain until recently, apparently without special study. The general aspect of the plant offers a strange commingling of individual characters of such genera as *Bidens*, *Coreopsis*, and *Cosmos*. The fruiting heads, with their elongate, rostrate achenes, are particularly suggestive of *Cosmos*. The marginal wings of the achenes and also the upward direction of the hairs or setae both upon the achenial bodies and upon the achenial aristae, however, might indicate more of an affinity with *Coreopsis*. For several years I have hesitated to describe this species lest, because of its bizarre combination of characters, it might later appear to have been described previously in some genus unsuspected by me.

Some time ago Dr. S. F. BLAKE, Associate Botanist of the United States Bureau of Plant Industry, kindly made for me a very careful and extended supplementary study of the plant in question. He concluded it to be a new species. Furthermore, he concluded that it was best regarded, not as typifying a new genus, but as being an extreme form in the genus *Cosmos*. My own study leads to the same conclusion. With the species of *Cosmos* as known up to the time of BENTHAM and HOOKER'S *Genera plantarum* (**2**:387. 1873) there appears a disagreement it is true, but some time later there was discovered the interesting *Cosmos exiguus* Gray (Proc. Amer. Acad. **22**:429. 1887). In *C. exiguus*, which beyond all question is to be retained in *Cosmos*, the purple rays, the foliage (in larger specimens closely approaching that of *C. linearifolius* [Schz. Bip.] Hemsl.), and the long-rostrate

achenes are typical of *Cosmos* as formerly restricted by definition; but the dense achenial hispidity, the upward direction of both the corporal and the aristal setae upon the achenes, and the obcompressed, more or less margined or winged achenial bodies, all are at variance with the older definitions of *Cosmos*.

It is seen that the BERNOULLI and CARIO plant closely parallels *C. exiguus* in its more notable characters, and, with it, must be placed in *Cosmos*. For the trivial name I have chosen to commemorate the name of Dr. BLAKE, to whom it is a pleasure thus to acknowledge my indebtedness for his painstaking study of the herbarium material.

Cosmos Blakei, sp. nov.—Herba erecta, verisimiliter annua, infra glabra, supra pubescens, caule obscure tetragono, internodis longo, tantum moderate ramoso, +5 dm. alto (radice non visa). Folia tenuiter petiolata petiolis 1.5 cm. longis, petiolo adjecto ±1 dm. longa, bipinnatisecta segmentis linearibus, acriter apiculatis, minute hispidis ac spinuloso-ciliatis, 0.5–1.5 mm. latis. Capitula ramos terminantia, robuste pedunculata pedunculis usque ad 1.2 dm. longis, radiata, pansa ad anthesin ±2.5 cm. lata et ±1 cm. alta. Involucrum pubescens, plus minusve campanulatum bracteis exterioribus spathulatis et supra saepe late rotundo-dilatatis, marginibus ciliatis apice aegre mucronatis, 4–6 mm. longis; interioribus multo maioribus, in sicco perspicue subflavis, late lanceolatis, ad apicem angustatum saepe minute glandulo-ciliatis, circ. 1 cm. longis. Flores ligulati circ. 8, tantum valde manci visi, in sicco atri vel obscure atro-purpurei, circ. 1.5 cm. longi; ovario lineari, membranaceo, sterili, in sicco nitido-albescente, marginibus et supra ad costam medianam erecto-hispido, corpore circ. 1 cm. longo, apice erecto-hispido et aegre aristato 1–2 aristis tenuibus sursum hispidis ±0.5. mm. longis. Flores disci corolla tantum circ. 5 mm. longi, in sicco flavi. Achaenia (multa matura visa) valde obcompressa et infra circumambitu (alis latis inclusis) perspicue oblanceolata, faciebus atro-brunneis glaberrima vel supra et ad costam medianam erecto-setosa, marginibus straminea et setis spinulosis minute erecto-ciliata, supra cervicata cervice substraminea erecto-ciliata plerumque 3–7 mm. longa, tota longitudine (usque ad cervicis apicem) 1.4–2.4 cm., latitudine (alis inclusis) 2.7–3.4 mm.;



SHERFF on COSMOS

apice erecto-hispida et biaristata aristis erectis vel parce divergentibus, tenuibus, sursum hispidis, 1.5–2.5 mm. longis.

Type specimen: *Bernoulli* and *Cario* 1476
Retalhuleu, Guatemala, January 1871 (Herb. Kew).

CHICAGO NORMAL COLLEGE
CHICAGO, ILL.

[*Accepted for publication February 24, 1926*]

EXPLANATION OF PLATE XXII

Cosmos Blakei: a, fruiting specimen, uppermost part, ×0.6; *b*, exterior involucral bract, ×3.6; *c*, interior involucral bract, ×3.6; *d*, ovary of ligulate floret, ×3.6; *e*, palea, ×3.6; *f*, disc floret, ×3.6; *g*, stamen, ×30; *h*, style-branches, ×22; *i*, *j*, achenes, ×3.6; *k*, transverse section of achene, ×7.2; all from *Bernoulli* and *Cario* 1476, type in Herb. Kew.

BRIEFER ARTICLES

STRUCTURAL WEAKNESSES IN INTERSPECIFIC GRAFTS OF PYRUS

(WITH ONE FIGURE)

More than twenty years ago WAUGH[1] published a paper on the nature of the union between stock and scion, especially in hardwood grafting. I have been unable to find anything reported since that time that adds materially to our knowledge of the nature of the finer structural details of the union of grafted woody plants. Because of the obvious importance of a more thorough understanding of the nature of this phenomenon, an attempt was made to determine the characteristics of the unions of several interspecific grafts, with the hope that this information may aid in our understanding of the observed results of such grafts.

WAUGH has adequately treated the gross characters of the graft, finding (1) that the scion and the stock never grow together; (2) that the new layers of wood are produced in continuous layers in normal or successful unions; (3) that in imperfect unions the continuity of xylem is interrupted to a greater or less degree by the deposition of scar tissue, which makes the union mechanically weak; and (4) that this irregular structure is due to physiological incompatibility. His figures show the clear line of cleavage between stock and scion in both good and poor unions. He gives a single figure showing detail of union, a tangential section of a cherry-plum graft.

The studies reported here have confirmed the observations of WAUGH on the gross characters of the union, and the frequency of the occurrence of weak unions in some combinations due to the laying down of parenchyma at the line of union. There is often in addition a severe distortion of the vessels lying in the region of the union.

In the course of this study, a condition was found that seems not to have been reported earlier. This arrangement of tissue is illustrated in fig. 1, which shows a graft union of *Pyrus Malus* on *P. communis*, a combination usually incompatible. Instead of the layer of parenchyma that is usually found in weak unions, or associated with such a layer, there is bark tissue. This bark may roughly be divided into three parts, a corky

[1] WAUGH, F. A., The graft union. Mass. (Hatch) Agric. Exp. Sta. Tech. Bull. 2. 1904.

layer in the middle, of indeterminate origin, and a layer of bark on either side. Each of these two layers is characteristic of the bark of its species. In this case the layer shown at the top of the figure is apple and that at the bottom is pear.

A gross examination of the union from which this section was taken discloses the fact that the layer of bark extends nearly to the point at

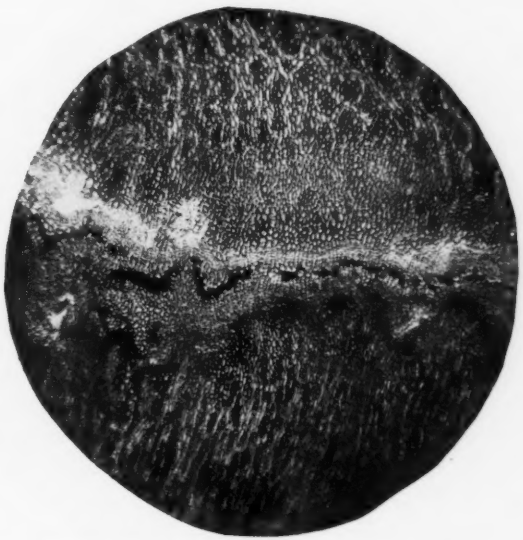


FIG. 1.—Tangential section of *Pyrus Malus* on *P. communis*, showing bark layers at line of union.

which the cambium layers of stock and scion were placed in contact at the time the graft was made. There has been enough movement of water and of nutrients through the relatively small amount of new tissue that is continuous to allow growth to proceed. It would appear that soon after growth had started, the region of the cambium which lay at the line of union ceased to function. As growth continued above and below, a layer of bark was laid down by the cambiums of both stock and scion. The result is a formation closely resembling in its final condition that described by MAC DANIELS[2] in narrow crotches. The layer of bark pinched between the

[2] MACDANIELS, L. H., The apple-tree crotch. Cornell Univ. Agric. Exp. Sta. Bull. 419. 1923.

xylem on either side forms a line of mechanical weakness. It is doubtful whether such a union would survive the second season, when a larger leaf surface would provide a greater resistance to wind movement and place a greater strain on the union.

The condition described has been observed in the following interspecific grafts growing as one-year old trees in the nursery: *Pyrus Malus* on *P. serotina*, *P. Malus* on *P. communis*, *P. communis* on *P. Malus*, *P. communis* (var. Bartlett) on *Cydonia oblonga*, and *C. oblonga* on *P. serotina*. It occurred in both budded and grafted material.

It should be stated that there is a high degree of variability among the grafts of a given sort as to the frequency of the appearance of this condition and its extent in a given union. Thus, in the case of *P. Malus* on *P. serotina*, there are gradations from perfect unions to those having a mere shred of continuous xylem. Whether this variability is due to genetic differences in the seedling stocks or to the mechanical treatment and environmental conditions of the graft is not known.

Studies with species of *Prunus* have not been carried far enough to determine whether or not this condition exists in that genus. A condition that is somewhat similar, however, appears frequently in the case of *Prunus domestica* on *P. Persica*. In this case the activity of the cambium at the line of union is not entirely inhibited but greatly reduced. The result is a very gradual development of the condition, which does not cause a high degree of mechanical weakness, but which does interfere with translocation and may cause the death of the tree.—E. L. PROEBSTING, *University of California, Davis, Cal.*

[*Accepted for publication February 26, 1926*]

CURRENT LITERATURE

BOOK REVIEWS

Applied paleobotany

During recent years a number of paleobotanical publications were published in Germany which dealt with practical and theoretical conclusions that can be drawn from plant fossils.

In the series of volumes which G. GÜRICH publishes under the title of *Leitfossilien*, the third volume deals with the Carboniferous and Permian, and the plant fossils which serve as horizon markers in these formations.[1] This book represents the most modern textbook of paleobotany with special reference to the stratigraphic distribution of plant fossils. Previously only one attempt has been made to treat in a textbook the fossil plants from the point of view of their geologic distribution. This was done by Sir WILLIAM DAWSON in his geologic history of plants in 1880, but DAWSON's book is obsolete by this time. GOTHAN has rendered a great service in writing a book which can be taken out into the field and used for determinations as well as for reference. Although he considers almost exclusively the fossil plants of the European Carbon and Perm, a great deal of this information can be applied and utilized in America, because of the great similarity between the Upper Carboniferous and Permian of the two continents.

More theoretical than GOTHAN's book is another one which appeared as no. 8 of SOERGEL's *Fortschritte der Geologie und Palaeontologie*.[2] He tries to show what we may learn from the fossil plants to apply to biology, especially in adaptation. The book is more or less a collection of essays, and does not attempt to give a comprehensive treatment of the paleobiology of plants. Of special interest are the chapters on the periodicity of growth and on the climatic problems as they confront us in a study of fossil plants. Primarily the floras of the Upper Paleozoic are consulted.

A very interesting volume[3] deals with the ability of plants to form rocks. PIA is familiar with this subject and has written a number of papers on calcareous algae. In the present volume he gives a detailed account of how strata can be formed through the activities of sulphur bacteria, iron bacteria, lime forming bacteria, unicellular algae, and organisms depositing lime or silica. Among the latter, of special interest are the diatoms. A chapter is devoted to

---

[1] GOTHAN, W., Karbon und Perm-Pflanzen. pp. viii+187. *pls. 45. figs. 144.* Berlin: Gebruder Borntraeger. 1923. $7.50.

[2] ———, Palaeobiologische Betrachtungen über die fossile Pflanzenwelt. pp. 178. Berlin: Gebrüder Borntraeger. 1924. $2.25.

[3] PIA, JULIUS, Pflanzen als Gesteinsbildner. pp. viii+355. *figs. 166.* Berlin: Gebrüder Borntraeger. 1926. $5.00.

the rôle which unicellular plants play in the formation of coal and petroleum. A detailed account is rendered of the green algae, brown algae, and red algae, which form lime deposits. This part of the book includes also lime forming mosses and angiosperms. Nearly half of the book is devoted to coal and its formation, while the larger portion of the author's discussion deals with the paleozoic coals. He also considers the floras which have formed the lignite beds and the peat bogs of past and present.

PIA discusses in his book primarily the rôle which plants have played in former geologic periods in the formation of strata, but he always uses extensively for his explanations analogies with recent plants. Bibliographies at the end of chapters are helpful, although rather restricted to the more important publications. The illustrations are excellent and very instructive. The entire book is of great interest, not only to paleobotanists, but also to students of living plants.—A. C. NOÉ.

Results of biological research

Among the most welcome books nowadays are those presenting summaries or digests of recent researches in the various fields of knowledge. The first of a new series of volumes of this character comes from Germany. The field covered is biology in general, with special emphasis on the comparative physiology and psychology of animals, plant physiology, the mechanics of development, and theories of inheritance. There are four editors responsible for the series, FRISCH of Munich, GOLDSCHMIDT of Berlin, RUHLAND of Leipzig, and WINTERSTEIN of Rostock.[4]

The articles, of which there are six in the first volume, are by specialists in the field presented. Three of the articles, taking up five-sixths of the volume, are zoological or psychological. The botanical articles are on (1) the ascent of sap, by BACHMANN of Leipzig; the reactions of the plant cell to salts, by KAHO of Dorpat; and ammonia, nitrate, and nitrite as sources of nitrogen for the higher plants, by PRIANISCHNIKOW of Moscow.

Most of the article on the ascent of sap is devoted to DIXON's cohesion theory in the light of the more recent researches; a few pages are given to the condensation theory of BAKER, the polarity and enzyme theory of JANSE, and the curious pulsation theory of BOSE. A characteristic and welcome feature of this and the other articles of the volume is an ample citation of literature. This new series should be in every library which is consulted by research workers in the fields the series covers.—H. C. COWLES.

Citrus diseases

A book on citrus diseases and their control, by FAWCETT and LEE,[5] will be the standard work in this field for some time to come, not only for those inter-

[4] FRISCH, K. VON, GOLDSCHMIDT, R., RUHLAND, W., and WINTERSTEIN, H., Ergebnisse der Biologie. Vol. I. 8vo. pp. viii+670. *figs. 130.* Berlin: Julius Springer. 36 marks; 38.40 marks bound.

[5] FAWCETT, H. S., and LEE, H. A., Citrus diseases and their control. 8vo. pp. xii+582. *figs. 205* (*15 in color*). New York: McGraw-Hill Book Co. 1926. $5.00.

ested in the scientific aspects of the subject, but also for those engaged in the production and marketing of citrus. Guided by the needs of growers and distributors, as well as by the requirements of investigators and teachers, the authors have of necessity been led to a more catholic concept and presentation of disease than is generally found in phytopathological literature. The authors squarely met the issue that a treatise on the pathology of a crop must be more than the applied mycology of that crop; consequently the volume takes up diseases due to animal and plant organisms as well as to non-living factors. The book is sound scientifically and pedagogically. The detailed description of the host of diseases that afflict all parts of the citrus plant in the grove and in the marketing processes is preceded by discussion of such fundamental topics as the species and varieties of citrus and their distribution in relation to disease; the normal structure and physiology of citrus as well as the relation of environmental factors to citrus culture and marketing, and to disease; and the nature and methods of control. The diseases are grouped for discussion on the basis of the organs affected, and under these headings useful keys are provided. The volume has all the earmarks of preparation by experts with firsthand knowledge of their subject matter. The literature is exhaustively treated, and the authors have taken commendable pains to give full credit to the many workers who have built up the structure of citrus knowledge. The volume is well printed and the illustrations, which are well chosen, are especially well done. The fifteen colored plates add materially to the usefulness and attractiveness of the book.—G. K. K. LINK.

The Cyanophyceae

A volume[6] has just appeared in the series of monographs on the fresh water flora of Germany, Austria, and Switzerland, which will be welcome to all who are working with the blue-green algae, for the group is so cosmopolitan that the keys work very well with the Cyanophyceae of the Chicago region.

The first fifty pages deal with the cytology, morphology, phylogeny, and biology of the group, while the rest of the book is devoted to keys and taxonomic descriptions, all of which are in German. The illustrations are excellent and many of them are new.

The number of families is greater than in KIRCHNER's treatment in ENGLER and PRANTL's *Natürlichen Pflanzenfamilien*, and it would seem that there is a tendency to raise the rank of some forms, but this does not detract from the real value of the book. Fewer and fewer botanists are reading Latin fluently, and consequently the German keys will make the book more usable than those with Latin keys; besides, the book is up to date.—C. J. CHAMBERLAIN.

---

[6] GEITLER, L., Die Süsswasser-Flora Deutschlands, Österreichs und der Schweiz. Heft 12. Cyanophyceae. 8vo. pp. viii+481. *figs. 560*. Jena: Gustav Fischer. 1925.

NOTES FOR STUDENTS

Taxonomic notes.—RILEY[7] has published a revision of *Calycolpus* (Myrtaceae), a tropical American genus. He recognizes 12 species, 6 of which are described as new.

CRAIB,[8] in continuation of his contributions to the flora of Siam, has described 28 new species, representing 16 genera, of which *Impatiens* includes 9.

KOBUSKI[9] has revised *Priva*, a genus originally segregated from *Verbena*. It is a tropical genus, 9 species being endemic in the western tropics, and the other 2 (one of which is described as new) endemic in the eastern tropics. One species only extends into the United States. The author has also included a very complete list of collectors and stations.

EPLING,[10] in his second contribution on the Labiatae of South America, has given a detailed account of the genus *Sphacele*, most of whose species are distributed along the western border. He recognizes 24 species, 3 of them being new.

GRENZEBACH[11] has published a revision of *Bouchea* (Verbenaceae), a small genus occurring chiefly in the Western Hemisphere, ranging from New Mexico to Bolivia. Only one species is known from the Eastern Hemisphere, occurring in Abyssinia. The 10 species include one that is new, and also 2 new varieties.

HONDA,[12] in continuation of his studies of the grasses of Japan, has presented 15 species in 8 genera, including 2 new species. The greatest changes occur in the varietal names, 18 new ones being proposed.

ITO and HOMMA[13] have described a new genus (*Miyabella*) of Synchitriaceae, including 2 species. It is a segregate from various genera of the family. The generic name is in honor of Professor K. MIYABE.

MERRILL[14] has published a second paper describing new plants discovered in the Philippines. It is based mostly on material collected in Bohol during August and September. It includes descriptions of 28 new species, in about as

[7] RILEY, A. M., Revision of the genus *Calycolpus*. Kew Bull. no. 4. 145–154. 1926.

[8] CRAIB, W. G., Contributions to the flora of Siam. XVIII. Kew Bull. no. 4. 154–173. 1926.

[9] KOBUSKI, C. E., A revision of the genus *Priva*. Ann. Mo. Bot. Gard. **13**:1–34. 1926.

[10] EPLING, C. C., Studies on South American Labiatae. II. Ann. Mo. Bot. Gard. **13**:35–70. 1926.

[11] GRENZEBACH, M., A revision of the genus *Bouchea*. Ann. Mo. Bot. Gard. **13**:71–100. 1926.

[12] HONDA, M., Revisio Graminum Japoniae. IX. Bot. Mag. Tokyo **40**:97–109. 1926.

[13] ITO, S., and HOMMA, Y., *Miyabella*, a new genus of Synchitriaceae. Bot. Mag. Tokyo **40**:110–113. 1926.

[14] MERRILL, E. D., Additions to our knowledge of the Philippine flora. II. Philippine Jour. Sci. **29**:475–496. 1926.

many genera, and also the establishment of 2 new genera of Rubiaceae (*Boholia* and *Sulitia*). The only fern represented is *Schizoloma cordatum*, which is recorded for the first time from the Philippines.

The British Museum is publishing, as a supplement to the *Journal of Botany*, a report of the collection of plants made by JOHN GROSSWEILER in Portuguese West Africa. The 24 pages issued (March-May) include about 90 species, representing 10 families of dicotyledons, of which about 30 are described as new. The largest family is Annonaceae, with 30 species, 12 of which are new; while the Cruciferae are represented by only a single species. The next largest family is Polygalaceae, with 21 species, 19 of them belonging to *Polygala*. The Menispermaceae are also well represented by 17 species, 5 of which are new. The remaining 22 species are distributed among 7 families.

GLEASON,[15] in continuation of his studies of the flora of northern South America, has described 10 new species from British Guiana, representing 8 genera. Two of the genera are published as new, namely *Tetrapodenia* (Malpighiaceae) and *Barnhartia* (Styracaceae).

RYDBERG[16] has published 2 new species from the mountains of West Virginia, *Aconitum vaccarum* and *Heuchera alba*.

SMALL[17] has described a notable new palm, *Sabal Deeringiana*, found growing in the Mississippi delta region. It had been referred to in 1857, in a report of the Mexican Boundary Survey, but "the clue was not followed up." It was recently "rediscovered by mere accident." SMALL[18] has also described a new endemic *Campanula* (*C. Robinsiae*) from Florida.—J.M.C.

Forests of Western Australia.—This part of Australia presents a wide range of climatic conditions within its 900,000 square miles. The rainfall varies from 6 to 70 inches per year, and results in a great variety of forest types which have been well described in recent articles by GARDNER.[19] This author distinguishes sclerophyllous forest in regions with more than 20 inches of rainfall, and among them includes (1) Karri forest, where the precipitation is rather evenly distributed throughout the year. Here the "Karri," *Eucalyptus diversicolor*, is the chief tree, reaching a height of 300 feet, with a lower story of *Agonis*, *Banksia*,

---

[15] GLEASON, H. A., Studies on the flora of northern South America. IX. Bull. Torr. Bot. Club **53**:289–301. 1926.

[16] RYDBERG, P. A., Two new species from the mountains of West Virginia. Torreya **26**:29–33. 1926.

[17] SMALL, J. K., A new palm from the Mississippi delta. Torreya **26**:33–35. 1926.

[18] ———, A new bellflower from Florida. Torreya **26**:35. 1926.

[19] GARDNER, C. A., The hardwood forests. Australian Forestry Jour. **6**:185–191. 1923. The forest formations of Western Australia. I: The Karri forest. II: The Jarrah forest. III: The Tuart forest. IV: The Wandoo forest. V: The Salmon gum forest. VI: The Mulga bush. VII: The Tingle-tingle forest. VIII: The Kimberly sclerophyllous woodlands. *ibid.* **6**:52–55; 104–108; 199–202; 296–300. 1923. **7**:38–45; 120–123; 256–259. 1924. **8**:4–6; 72–75. 1925.

Casuarina, *Acacia*, and *Albizzia*, 30–40 feet high; and (2) Jarrah forest, where the rainfall is somewhat more periodic and the "Jarrah," *E. marginata*, grows in rather close stands 75–100 feet high, with an understory of smaller trees. The wood of this Jarrah is hard and durable, being sometimes known as Australian mahogany.

Where the rainfall is 15–20 inches a savanna forest develops, with trees 50 feet high and a grassy undergrowth. Here there are various species of *Eucalyptus*, *Agonis*, and *Acacia*. With less rainfall the vegetation may consist either of poorer savanna or of "mallee scrub," consisting of small scrubby species of *Eucalyptus*, or "Mulga scrub," consisting of *Acacia aneura* and its associates.

The ecological, forestry, and economic relations of the various types are well considered.—GEO. D. FULLER.

Sulphur bacteria.—In a paper which adds little of empirical or theoretical value to our knowledge of the sulphur bacteria, BAAS-BECKING[20] describes an ecological community or association of organisms living on the black mud of California lakes. The association is called a sulphuretum, and is limited to alkaline substrates of varying salinity. Nine genera of endothio-bacteria have been found in the region.

The author believes that H_2S is incapable of furnishing the energy for their metabolism, but that it is the HS- ion which serves as the material for oxidation and energy yield. All observations agree with WINOGRADSKY'S classical researches of 40 years ago.

The formation of liquid sulphur globules in the bodies of these bacteria by oxidation of the hydrosulphide ion is interpreted in terms of the glutathione theory of HOPKINS. The reactions tentatively suggested are that oxidized glutathione reacts with HS- ion to form reduced glutathione and liquid sulphur, Sλ, which appears as droplets within the bodies of the endothio-bacteria. The process of chemosynthesis is thought possibly to involve the interaction of reduced glutathione with H_2CO_3 in such a way as to form H_2O_2 and the oxidized form of glutathione. In this reaction the H_2CO_3 is reduced to HCHO, presumably, which is then condensed to carbohydrate.

The H_2O_2, on being decomposed by catalase, might furnish oxygen in a form capable of oxidizing the stored sulphur to SO_4. The suggestions are only tentative, and not very convincing. There seems to be no inherent reason why both ions of the H_2S molecule might not supply hydrogen for the reduction of glutathione.

An error that should have been avoided is the inadvertent one of making glucosamine instead of glutamic acid a part of the glutathione molecule.— C. A. SHULL.

---

[20] BAAS-BECKING, L. G. M., Studies on the sulphur bacteria. Ann. Botany **39**:613–650. 1925.

Cambridge University Press

Monocotyledons. A Morphological Study. By AGNES ARBER, M.A., D.Sc. With a frontispiece and 160 illustrations. Large Crown 4to. $7.00. (*Cambridge Botanical Handbooks.*)

Devonian Floras. A Study of the Origin of Cormophyta. By E. A. NEWELL ARBER, M.A., Sc.D. With a Preface by D. H. SCOTT, F.R.S., a frontispiece, and 47 text-figures. Demy 8vo. $6.00.

The Classification of Flowering Plants. By ALFRED BARTON RENDLE, M.A., D.Sc., F.L.S., Keeper of the Department of Botany, British Museum. Vol. II. Dicotyledons. With 279 illustrations. Demy 8vo. $8.00.

A Dictionary of the Flowering Plants and Ferns. By J. C. WILLIS, M.A., Sc.D., F.R.S. Fifth edition, revised. Crown 8vo. $9.50. (*Cambridge Biological Series.*)

British Grasses and Their Employment in Agriculture. By S. F. ARMSTRONG, B.A., F.L.S., of the School of Agriculture, Cambridge. With 175 illustrations. Demy 8vo. $4.25.

The Ferns (Filicales). Treated comparatively with a view to their natural classification. By F. O. BOWER, Sc.D., LL.D., F.R.S. Vol. I, Analytical Examination of the Criteria of Comparison. With a frontispiece and 309 illustrations. Royal 8vo. $10.00.

Plant Life on East Anglian Heaths. Being Observational and Experimental Studies of the Vegetation of Breckland. By E. PICKWORTH FARROW, M.A., D.Sc. With 46 illustrations. Crown 4to. $2.50.

The Anthocyanin Pigments of Plants. By MURIEL WHELDALE ONSLOW, M.A. Second edition. Royal 8vo. $7.00.

Experiments in Genetics. By CHARLES C. HURST, Ph.D. (Cantab.). With 174 illustrations and a map. Large Royal 8vo. $16.50.

Botany: A Junior Book for Schools. By R. H. YAPP, M.A. (Cantab.), Mason Professor of Botany in the University of Birmingham. Second edition. With 159 text-figures. Crown 8vo. $1.20.

Botany: A Textbook for Senior Students. By D. THODAY, M.A., Lecturer in Physiological Botany, University of Manchester. Third edition. With 230 text-figures. Crown 8vo. $3.50.

Life. An Outline of Biology. By SIR A. E. SHIPLEY, G.B.E., F.R.S. Second edition. With 71 illustrations. Crown 8vo. $2.50.

Published by the Cambridge University Press (England)

The Macmillan Company, Agents in the United States

60 Fifth Avenue, New York City

The Modern Way to Write

is on a

Remington Portable

The smallest, lightest, and most compact of all standard keyboard portable typewriters.

Remington Typewriter Company

374 Broadway, New York

Branches Everywhere

Rhus Dermatitis

Its Pathology and Chemotherapy

By JAMES B. McNAIR

¶ The lack of any rational treatment for the common infection resulting from poison oak or poison ivy has suggested a protracted study of the isolated principle, in the hope that knowledge of its characteristic properties may serve as a basis for such treatment.

¶ Complete analysis of cause, effect, and remedy has been attained by investigating from the three distinct standpoints of pharmacology, botany, and chemistry.

$4.00, postpaid $4.15

The University of Chicago Press
Chicago - - - Illinois

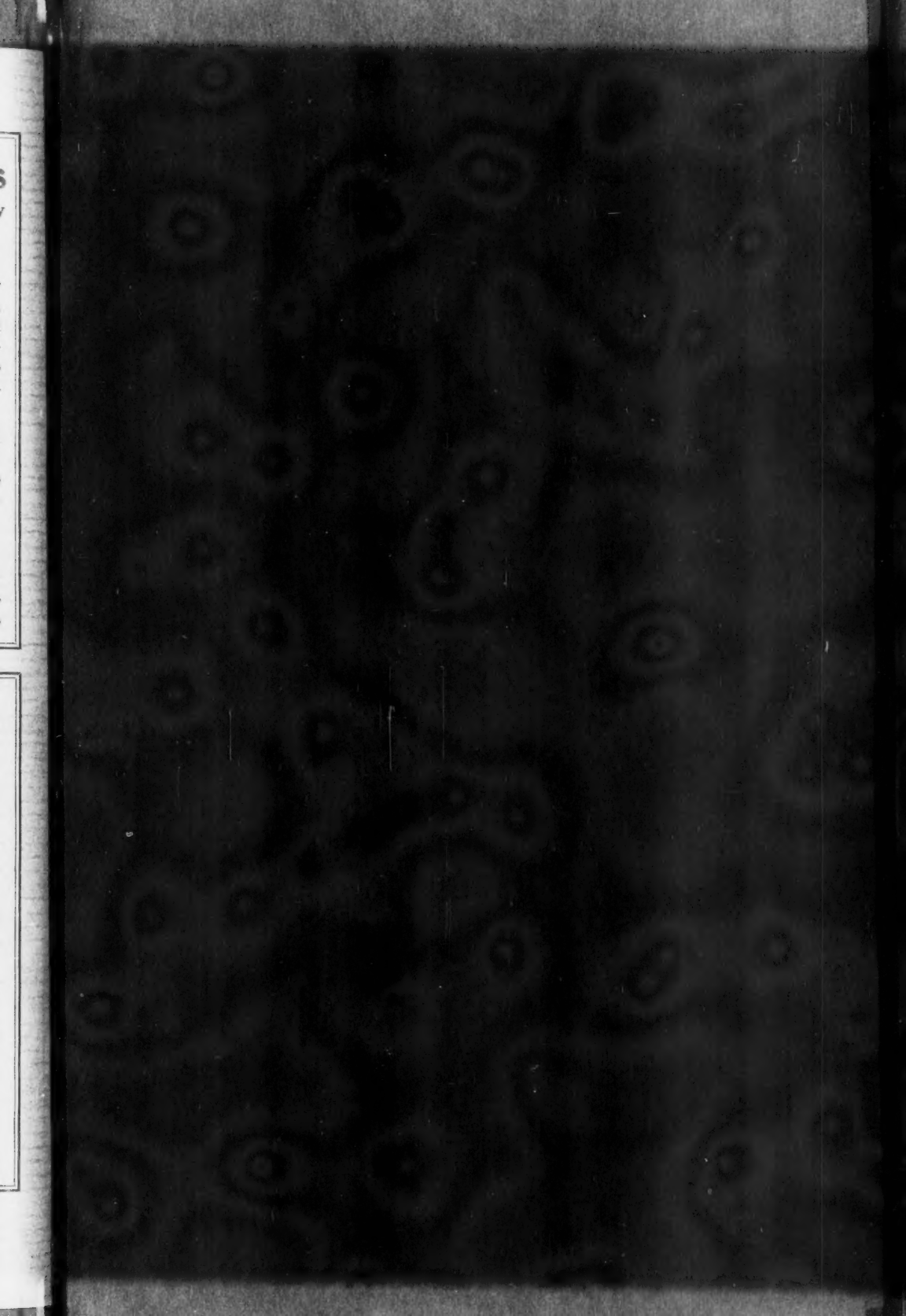
The Anatomy of Woody Plants

By E. C. JEFFREY

Jeffrey, the leading authority on plant anatomy, is the most original investigator in this field since the great DeBary. This is a standard work on the subject—the only recent book to compare with DeBary's classic.

It does for the anatomy of plants what has long been done for human anatomy. Paleobotanical evidence figures largely, and the book is equally valuable to the paleobotanist, the morphologist, and the general student.

"Its value as a textbook in the anatomy of woody plants is of signal importance."—*Scientia.*

Illustrated $4.75, postpaid $4.87

THE UNIVERSITY OF CHICAGO PRESS
CHICAGO · ILLINOIS